# Principles and Methods in Landscape Ecology

## Towards a Science of Landscape

*by*

Almo Farina

Springer

Landscape Series

# PRINCIPLES AND METHODS IN LANDSCAPE ECOLOGY

# Landscape Series

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*by*

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# Foreword by the series editors

*Principles and Methods in Landscape Ecology* is already a classic among the books published around the world on the topic. In the foreword of the first edition, Zev Naveh wrote: “I am confident that this book will serve very well as both a textbook and as a handbook for those involved in landscape ecological study, research and education, as well as for many others from closely related fields of natural and human sciences dealing with land use”. Two years later, in the foreword of the other book of Almo Farina – *Landscape Ecology in Action* – Frank Golley wrote about *Principles and Methods*: “My students like this text especially well because it is direct, to the point and comprehensive. ‘Farina’ is on loan much of the time”.

It appears that the book is so successful that a new version is now necessary, and it is a real pleasure to include it in our Springer Landscape Series. The aim of the series is to highlight the diversity of landscapes and approaches used in their study. While the multiplicity of relevant academic disciplines and approaches is characteristic of landscape research, we also aim to provide a place where the synthesis and integration of different knowledge cultures is common practice. Such aims are possible only if principles and methods of Landscape Ecology are clearly understood by students and practitioners in the field.

Almo Farina was particularly qualified to write such a book. First, because of his personal involvement in education and in research and second, because of his intelligence of the needs of the international community: Almo served as the secretary of IALE, the International Association of Landscape Ecology as well as the general secretary of INTECOL, the International Association of Ecology for which he organized a memorable VII World Congress in 1998 in the city of Florence, Italy. In addition, what gives this book its strength and unique character is the deep involvement of its author in the issue of the future on landscapes around the Mediterranean Basin – a hotspot for biodiversity and for the natural and societal impacts of global environmental change.

*Principles and Methods in Landscape Ecology* clearly summarizes the best theories, concepts, principles and methods in landscape ecology. It is an important tool not only for classrooms, but also for a broad range of scientists and practitioners, particularly in the first decade of this new Millenium, when unprecedented digital representations of the Earth revolutionize spatial thinking and when, at the same time, landscapes experience drastic transformations triggered by unprecedented natural and societal changes everywhere in the world.

Toulouse and Aberdeen, February 2006

Henri Décamps
Bärbel Tress
Gunther Tress

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# Preface to the 2nd edition

Landscape ecology has greatly gained reputation and scientific visibility as theoretical and applied science as well, since “Principles and Methods in Landscape Ecology” was firstly published in 1998. Ecologists and practitioners have widely applied the principles of the landscape ecology to model and to manage disturbed landscapes and menaced pristine areas as well.

A revision and an integration of the contents of the former edition have been carried out with the aim to update epistemological concepts and theoretical contents, and to include updates of the recent relevant literature. A new sentence “Toward a science of the landscape” has been added to the title “Principles and methods in landscape ecology” in order to better figure out and to stress the tremendous progresses achieved by this discipline in ecological as well as in social and economic realms.

In this new edition a special emphasis has been reserved to the “biocomplexity” paradigm relocating the landscape processes into the family of non linear amd self-organizing phenomena. In particular, the first and the second chapter have been deeply integrated by new arguments dealing with the perception of the landscape.

The cognitive component of the landscape has been discussed in detail considering the different theories developed about the cognition and the environmental psychology. The paradigm of the eco-field, the bio-semiotic approach and the information theory, have been new arguments added to the original version.

Special attention has been reserved how landscapes behave and develop - the landscape ontogenesis hypothesis - incorporating the uncertainty and the hierarchical structure into the landscape paradigm.

Finally, a relevant goal of this new edition is create confidence in the new generations of students and practitioners to considering the ecological systems as the result of the integration between ecosystemic (non spatial) and landscape (spatial) patterns and processes.

# Preface

Currently considered bridge between basic and applied ecology landscape ecology occupies a new important "niche" in ecology representing a new star in the "galaxy" of the ecological sciences.

But the broad spectrum of his conceptual and methodological approaches has created a non-focused science strongly influenced by the more dominant disciplines like landscape planning and restoration, forest management, landscape architecture, etc.

The uncertain position of the landscape ecology among the ecological disciplines is in contradiction with the general reconnaissance that landscape dimension is a spatial scale in which important ecological processes occur. And the landscape is becoming very popular in many ecological related fields from plant disease to animal behavior.

Actually a consistent literature covers most of the landscape ecology themes and the theoretical frameworks are enough convincing to delineate new approaches and interpretations of the ecological complexity.

The available literature is growing very fast representing the different approaches by which the landscape ecology issues are addressed. But as in many other pioneering disciplines a general framework common to all users is lacking and the topics often are moving from a human oriented landscape ecology to simply large scale ecology.

In fact two souls are living in the landscape ecology the first is connected to the European culture and longer-time experience in landscape ecology especially in the field of landscape evaluation, management and restoration. A second soul is grown in the North America in the last two decades, characterized by theoretical basis and sophisticate methodologies producing formidable schools to study complexity beyond the ecosystem scale.

The presence of these two approaches in some measure is positive and allows the interchange of experience and point of views that found in exciting international meetings the main occasion.

In fact in the last decade landscape ecology has found a flowering of cultural initiatives aggregated around the International Association for Landscape Ecology (IALE) and a multitude of working groups in local Ecological Societies and in other NGO organizations have been successfully established.

Two possibilities exist to expand the landscape ecology, one consists in developing new researches, the last to develop a good educational framework. Both are important and non in conflict. With this spirit I have prepared this book aimed to summarize the best theory, concept, principles and methods in landscape ecology. An attempt to reinforce the landscape ecology approach in the ecological research perspective, to consolidate principles and methods, in validating procedures and to riconciliate different positions including geobotanic, animal and human perspectives.

The conceptual scheme is very simple. The direct address by which I move dealing with the landscape ecological issues is necessary to reduce the "fringes" that often characterize some compartments of this discipline.

I have no ambition to present new ideas and theories, I have worked to wrap up a tool spendable mainly in classrooms but also for orienting a broad range of scientists and practitioners dealing with the landscape complexity and related problems.

The selection of a simple and contemporarily enough "objective" conceptual path is full of risks due to a personal interpretation of this discipline. Theoretical basis, the contribution of other disciplines, emerging processes and patterns, managing applications and methods are the main steps that I have utilized in this exciting journey.

The book is not comprehensive neither for topic nor for references, but this has not been my goal.

I have tried to maintain a good balance between the relevant literature offered but often my background of "naturalist" has prevailed. In any way the percentage of literature for the different topics has been respected and it is not a surprise that animal studies are dominant in landscape ecology.

The references are not comprehensive but essential to "cover" the argument taken into consideration. In some cases has not be easy to make the best choice either for the great number of studies (f.i. on the effect of fragmentation on animal populations) in other cases for too few studies available (soil landscape and flux of nutrients in the landscape).

Some comments are necessary to explain the general project of the book with the sincere hope to do not bore the reader from the beginning .

In the short introduction to the landscape ecology I have avoided too "long historical perspectives" focusing more on the real object of the landscape ecology and on good definitions.

I have underlined the contribution of other related ecological disciplines in the creation of a strong conceptual framework.

The description of new theories as percolation, metapopulation, hierarchy, etc. have preceded the scaling approach.

Emerging processes (fragmentation and disturbance, connectivity and ecological fluxes) and patterns (heterogeneity and ecotones) occupy the central part of the book.

Landscape dynamic, management and nature conservation at landscape scale have been extensively described.

The last chapter is fully devoted to methods. Special importance has been maintained to indices describing the structure of the landscape mosaic from Euclidean to fractal geometry. GIS and GPS procedures have been included as indispensable tools. Remote sensing procedures and spatial explicit models occupy the final part of the book. In addition very simple routines to measure landscape structure and complexity are presented. These routines may be improved and incorporated in more sophisticate programs. I have tried to encourage people to measure the landscape by using simple tools aware of the frustration felt by people reading about huge, expensive and powerful computation and remote sensing facilities of super-specialized advanced research centers.

I am perfectly aware about the limit of this book, I am conscious that many perspectives have not been discussed like the socio-economical implications.

Most of the pictures and examples are from my preferred study area (Northern Apennines, Italy). The environmental and cultural complexity of this region, like most of Mediterranean basin is an exciting field to test and apply landscape principles and methodologies and an inexhaustible source of scientific creativity.

I am in debt with many people and in particular to Zev Naveh for his invaluable encouragement. I am grateful also to Francesco Di Castri for his friendship and the support during the preparation of this book.

# Foreword

Landscape ecology has its roots in the long tradition of central and eastern European geobotanists, ecologists, geographers, landscape planners and architects who were not content with the present state of their sciences and profession.

They strived to present their rich and heterogeneous landscapes in more holistic ways, as the spatial and functional integration of nature, humans and land, so that their studies could be of practical value in landscape appraisal, planning, management, conservation and restoration.

However, chiefly because of language and cultural barrier it remained a rather restrict "continental" science until it was joined more than twenty years ago by the "second generation" of a large group of far-sighted - and chiefly North American – ecologists and geographers. These realized the theoretical and methodological relevance of landscape ecology and the need for broadening the spatial scales of ecosystem ecology for the study of the ordered complexity of natural and cultural landscapes.

The two groups joined together and founded the International Association of Landscape Ecology (IALE). Fortunately these developments coincided with the dramatic advances in remote sensing and satellite imaging with finer and finer resolutions over larger and larger areas and with the progress in processing larger masses of data in smaller and cheaper computers with more sophisticated and comprehensive modelling methods. Since then landscape ecology has spread its wings all over the world both in industrialized and developing countries as one of the youngest and most dynamic branches of contemporary environmental science.

The author of this book, Dr. Almo Farina, is the first of the "third generation" who not only followed the footsteps of both these founder groups but contributed a new milestone to its further development and especially to the education of the next generation of landscape ecologists, academians and professionals. He took upon himself the challenge to provide a meaningful synthesis of what he consider to be the "best theory, concept, principles and methods" which are presently applied in a multitude of landscape-ecological studies and are published in the journal "Landscape Ecology" and in many other journals and scientific publications.

Presenting in a lucid way some of the most relevant new ideas, theories and paradigms, he succeeds also in reconciling the diverse geological, biological and human perspectives. At the same time he provides his own original well-versed and well-balanced contribution to contemporary landscape ecology as a holistic, quantitative and problem-solving oriented science for the promotion of sustainable, healthy and productive landscapes.

Although dealing in a systematic way with a large body of rather complex scientific information, such as fractal dimensions, numerical and spatial data processing and geographic information systems, this book is far from being dry, technical and detached from reality. On the contrary it is very lively with many fine illustrations and with many practical examples. While reading through its chapters I could sense that it was written by one who is eager to communicate not only his own knowledge and holistic perception of landscapes as a hybrid nature-culture gestalt systems, but also his close personal attachment to the biological and cultural assets of his Appenine mountain and rural landscapes in which he grew up, and lives and works, and where he carries out his own research.

A great advantage, in my opinion, is the fact that this book was not written by a purely academic scientist, spending most of his time sitting in an office behind a computer, trying to publish as many possible "scholarly" works to further his own reputation. Dr. Farina started his professional career as a high school teacher in biology and is still very active in public education as Director of the Lunigiana Museum of Natural History at Aulla, Italy (Which was established and is maintained thanks to his initiative to preserve one of the most outstanding historical landscape monuments of this region). He started his research as an enthusiastic ornithologist but very soon realized the great potentials of landscape ecology, which fitted very well with his deeply ingrained perception of the landscape as a whole, and his intellectual abilities for acquiring the most advanced methods available and to turn these into practical tools for the study, management and conservation of landscapes. Dr. Farina is not only active in these local issues but is also deeply involved in the broader issues of the future of Mediterranean landscapes in Italy and in the Mediterranean Basin. He also served for four years as secretary of IALE.

I am confident that this book will serve very well as both a textbook and as a handbook for those involved in landscape ecological studies, research and education, as well as for many others from closely related fields of natural and human sciences dealing with land use. I am also hopeful that it will help to bridge the gaps between these different fields so that landscape ecology ca be realized as one of the most important integrative environmental sciences in this crucial transition period from the industrial to the information age.

Zev Naveh
Haifa, Israel

# Chapter 1

# INTRODUCTION TO LANDSCAPE ECOLOGY

## 1. 1 INTRODUCTION

Landscape ecology is one of the youngest branches of the ecology. It evolved after the World War II in the countries of Central and Eastern Europe (Schreiber 1990) and only recently expanded into America (Forman 1990) and Asia, assuming the definitive character of a distinct, unique, dynamic and integrated global science.

The roots of this discipline lie deep in geography as well as in geobotanic and land management. Two hundred years ago, the German geographer and scholar, Alexander von Humboldt, regarded the landscape as “the total character of a region”.

The term “Landscape ecology” was coined by the German biogeographer Carl Troll toward the end of 1930s. Troll hoped that a new science could be evolved combining the spatial “horizontal” approach of geographers with the functional “vertical” approach of the ecologists.

Landscape ecology, born as a human-related science (Naveh & Lieberman 1984, 1994), has recently been accepted by ecologists as a very promising level of ecological study (Risser et al. 1984; Forman & Godron 1986; Turner 1989; Farina 1993; Wiens et al. 1993; Forman 1995; Farina 1998, 2000; Moss 2000; Turner et al. 2001) (Figure 1.1).

Landscape paradigms are often utilized to explain complex phenomena like the transmission of diseases. For instance, landscape configuration has been found to be one of the relevant factors affecting the transmission of hantavirus in deer mice (*Peromyscus maniculatus*) (Langlois et al. 2001). The epidemiological models must take into account not only the demographic

*Figure 1-1.* Ecologists who have contributed to the foundation of the landscape ecology as an important branch of the ecological science:
(a) Carl Troll; (b) Frank Golley; (c)Wolfgang Haber; (d) Zev Naveh; (e) Richard Forman; (f) Isaak Zonneveld; (g) John Wiens. But many others have been relevant to the seed and affirmation of the landscape ecology world wide.

structure of the host population but the spatial structure as well. And this spatiality is the result of interaction with a land mosaic.

Moreover, the landscape ecology principles have also been used to interpret the spring phenological phases of plants that seem to have a relationship with landscape features (f.i. Ahas & Aasa 2001). The landscape paradigms are used to verify, for instance, the impact of organisms like large herbivores on the structure and spatial configuration of landscape (Barnett & Stohlgren 2001)

In 1986, principles and methods were introduced to a large ecologist audience on the occasion of the IV International Congress of Ecology in Syracuse, NY. Since then the presence of landscape ecology sessions in international congresses of ecology has become a rule (Farina 1999). Contemporarily, the intense activity of the new International Association of Landscape Ecology (www.landscape-ecology.org) has assured a continuum of international congresses and symposia.

The birth and the development of landscape ecology has been a progressive, dynamic and global process (Wu & Hobbs 2002) that has crossed and fertilized many fields of the ecology and related sciences including geography, botany, zoology, animal behavior, cognitive ecology and landscape architecture.

The landscape perspective is full of promises for the realization of the integration of different environmental and human-related disciplines into a "landscape science" (sensu Zonneveld 1990). The functional scale of landscape implicitly comprises a complete set of socio-economical and ecological processes.

During recent years, special attention has been paid to bio-complexity as a general framework in which landscape ecology can find a very important role. The complexity issue is today at the center of theoretical and empirical attention (Kauffman 1993; Merry 1995; Cilliers 1998; Lewin 1999; Bossomaier & Green 2000; Manson 2001; Weng et al. 1999).

The landscape includes most of the characters that define a complex system and several models are employed to illuminate processes related to landscape as a common basis (Li 2000, Farina 2004).

The change of approach from the study of ecosystems considered in their distinct and relative homogeneity to the landscape probably depends on the core of unresolved questions and shaded areas that the ecosystem approach has maintained during the last decennia, as O'Neill (2001) has critically argued. The ecology is aware of the potential role of interfaced disciplines, as recently pointed out (Klink et al. 2002). Space is recognized as a new frontier of ecology and landscape represents one of the main components of this "space" (Thompson et al. 2001).

## 1.2 THE CONTRIBUTION OF DIFFERENT DISCIPLINES TO THE CREATION OF A PARADIGMATIC FRAMEWORK IN LANDSCAPE ECOLOGY

The reconnaissance of the landscape as a suitable spatial scale on which to investigate ecological development has been a complicated process rooted in apparently distant theories. In our opinion the theory of island biogeography (MacArthur & Wilson 1967) and the focus on ecological geography (MacArthur 1972) are two fundamental events that have opened the road to modern landscape ecology.

The fact that space is an important component in determining the diversity of life forms and that most of the ecological patterns and processes have unique shaping factors may be considered the most influential paradigms to introduce space into the ecology as a fundamental element "per se" (Silbernagel 2003).

The presentation of ecological systems as components of a nested hierarchy (Allen & Starr 1982; O'Neill et al. 1986) has strongly contributed to linking different paradigms and theories incorporating the concept of scale. Contemporarily, new concepts such as fractal geometry have been introduced into the ecological realm (Mandelbrot 1975; Milne 1991,1992,1995; Jonhson et al. 1995; Milne et al. 2000) to investigate the complexity of nature. For instance, the complexity of ecological interactions has long discouraged ecologists from considering most of the more important interfaced ecosystems like coasts and marshes.

New ideas about the heterogeneity (Kolasa & Pickett 1991) and role of the disturbance regime (Pickett & White 1985) in ecological processes represent further progress on which paradigms like ecotones (Hansen & di Castri 1992; Naiman & Decamps 1990; Gosz 1993; Risser 1995), related processes like connectivity (Merriam 1984), theories like the metapopulation (Gilpin & Hanski 1991; Hanski & Gilpin 1991, 1997; Hanski 1999), and the percolation theory (Stauffer 1985; Ziff 1986) have been implanted. As a consequence of the recognized heterogeneity of the landscape, the sources-sinks paradigm developed by Pulliam (1988, 1996) recognizes and assigns new roles to the patches composing the landscape mosaic.

Information theory (Stonier 1990,1996), bio-semiosis (Hoffmeyer 1997; Kull 1998a,b; Nöth 2005) and autopoiesis (Maturana & Varela 1980; Maturana 1999,) are also useful topics to approach the landscape as a complex, self-regulating system.

The landscape scale and concept appear frequently in scientific literature ranging from soil science (Buol et al. 1989) to current perspectives in geoecology (Huggett 1995) and geomorphology (Malanson 1993).

Finally, landscape ecology is one of the most promising ecology-related disciplines, highly differentiated but with a common soul, based on the finite dimensions of the studies, a more precise overlapping of data and processed information in the real world and in the new "virtual" processes linked to information transfer on a global scale.

## 1.3 DEFINITIONS OF LANDSCAPE (A GALLERY)

Landscape ecology is too young to allow unique definition and concepts. Later, we will clarify the reason for this "tolerance" in the light of the complexity framework. We have to accept these premises and respect a wide core of disciplinary experiences in geography, geoecology, geobotany, ecology, behavioral ecology, landscape architecture and planning, Anthropology, Cognitive sciences, Biosemiotics, Environmental Psychology and Aesthetics, which converge in the direction of landscape ecology or find the landscape as a common meeting place.

For this reason, there are several definitions of landscape from different cultural and scientific approaches:

- “the total character of a region” (von Humboldt);
- “landscapes will deal with their totality as physical, ecological and geographical entities, integrating all natural and human (“caused”) patterns and processes . . . (Naveh 1987);
- “landscape as a heterogeneous land area composed of a cluster of interacting ecosystems that is repeated in similar form throughout (Forman & Godron 1986);
- a particular configuration of topography, vegetation cover, land use and settlement pattern which delimits some coherence of natural and cultural processes and activities” (Green et al. 1996);
- Haber (2004) has defined the landscape “a piece of land which we perceive comprehensively around us, without looking closely at single components, and which looks familiar to us”.

We find this last definition more broad than the others and also more suitable to be used to define the landscape as an entity “perceived” by all other organisms (from plants to animals). This opens a promising field of new research and speculations on the importance of the spatial arrangement of patterns and processes for the functioning of organisms, groups and ecosystems.

Most of the actual landscape ecology deals with human-modified ecosystems; this is inevitable due to the widespread distribution of human populations across the earth. But a broad range of ecological processes in pristine areas could also be efficiently approached using landscape ecology principles.

Landscape ecology is the study of complex systems, but needs to be referenced to an organism to be better understood, as argued by Turner et al. (1995). The landscape perceived by humans is different in size from the landscape perceived by a beetle (Wiens & Milne 1989). Hence, when the organism is man, the landscape is a broad area composed of a mosaic of patches, ecotopes and cultural elements (Figure 1.2). When we are dealing with the beetle’s landscape, we are necessarily reducing the physical and biological entity to a beetle’s alleged perception of the landscape.

The landscape ecology offers an extraordinary opportunity to carry out new epistemological and empirical experiments in which the contribution of different disciplines is essential. For this reason, several landscape ecologies are available today, from the more sophisticated in which human perception is compared with natural processes, to the more “simple” in which the ecology is approached using an enlarged spatial scale.

Finally, it is essential to clarify all these perspectives in order to reduce confusion and contradictions and to find a robust theory on the “landscape”. For this reason, in this revised edition, we have added a new section devoted to the epistemological approach, to illustrate information theories and semiotic fundamentals.

*Figure 1-2.* Large-scale aerial view of the Padana plain close to Bologna (Northern Italy). The spatial arrangement of fields, roads, buildings create a land mosaic called "landscape". At this resolution it is possible to distinguish the spatial and temporal organization of cultivated land.

## 1.4 AN EPISTEMOLOGICAL APPROACH TO THE LANDSCAPE

Due the complicated and different roots, the study of landscape ecology may be approached in several ways. Relevant books on landscape ecology have emphasized this fact in introductory remarks (Naveh & Lieberman 1984; Forman & Godron 1986; Forman 1995; Zonneveld 1995; Farina 1998, 2000). It is time to reconcile the different approaches to the evolution of landscape ecology. Historically, this discipline was born at the human perceived level and the first descriptions of families of processes were strictly linked to human life. With the recent development of landscape ecology as the study of the spatial arrangement of patterns and processes dealing with soil, vegetation, animals and humanity, a formidable bubble has been burst, especially in North America.

Despite the tremendous progress in the empirical field, landscape ecology shows a permanent fragility on the theoretical side. During the last ten years, new tools and a lot of investigations have clarified many aspects of the relationships between geographically perceived patterns and ecological processes, but very few attempts have been made to increase the theoretical framework (Wiens 1992; Antrop 2001; Tress & Tress 2001; Haber 2004) (Figure 1.3).

We consider it to be of great importance to include the landscape ecology into the paradigm of the General System Theory (von Bertalanffy 1969) and more generally, under the umbrella of complex systems (Farina 2004).

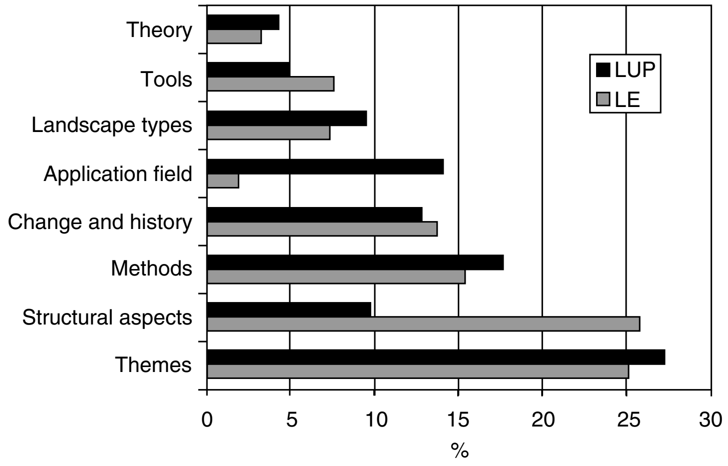


*Figure 1-3.* Importance (%) of main concept groups noted in the Landscape Ecology Journal (LE:1987-1999) and in Landscape and Urban Planning (LUP: 1986-1999) (from Antrop 2001, with permission).

Below, we will address our vision of the landscape according to a distinct epistemological perspective (Figure 1.4). We recognize at least three distinct levels:

The nature of landscape
The role of landscape
The description of landscape

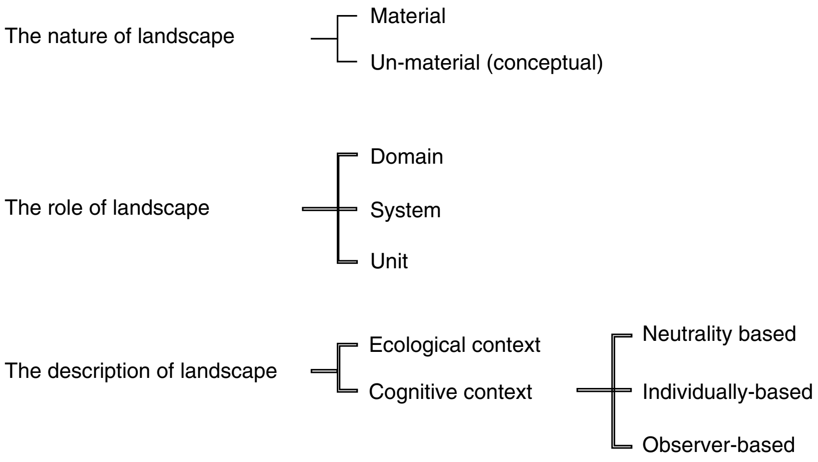


*Figure 1-4.* The epistemology of the landscape according to three approaches: nature, role and description (see text for details).

### 1.4.1 The nature of landscape

Landscape can be considered both as a material and un-material entity in which conceptual properties are integrated into physical properties. The material components are represented by the physical context of organisms and their aggregations. The un-material component is expressed by information (Stonier 1990, 1996) that can appear with different levels of organization. In the following pages and chapters, we will try to separately maintain the word "landscape" (a combination of material and un-material properties) and the word "mosaic", which represents the material component alone. However, this promise will not be maintained everywhere due to the impossibility to distinguish this vision when other authors are directly quoted.

### 1.4.2 The role of landscape

In order to solve the problem of linking together the un-material and material components of a landscape, we have to consider the landscape from at least three different perspectives: landscape as a domain; landscape as a system; and landscape as a unit (Figure 1.5). This different vision should not be considered as a problem but a confirmation that complexity does not have a unique address but a "family" of possible paradigms. Finally, complexity is not *per se* self-explaining and it is necessary to use theories, paradigms and models and just a small piece of complexity at a time can be disclosed.

#### *1.4.2.1 Landscape as domain*

The domain is the universe in which a process evolves or is maintained (Farina 2004). If we consider the landscape as a "gestalt" entity, composed of conceptual and physical components, the landscape domain is the field of existence of all the processes and related patterns. Nested into the landscape domain we find subdomains, which can be aggregated into distinct families producing

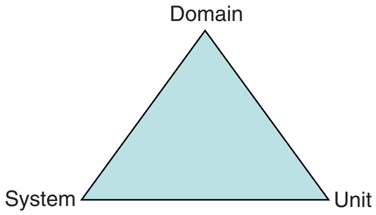


*Figure 1-5.* The three different possibilities to define a landscape under the umbrella of complexity.

meta-domains. We can try to describe these subdomains as an attempt to interpret the portion of complexity impounded by the landscape domain. We describe at least three hierarchical levels of subdomains. The first level shares the competencies between the physical and the conceptual realms. The second level is represented by the macro-processes (economics, religion, culture, environment). The third level is shared by the disciplines (ecology, geology, ethology, management, social sciences). Every level contributes to explaining certain components of the overall complexity. We consider the landscape as the largest container of the explicit complexity. This vision could seem too far from everyday empirical science but must be considered as one of the most important epystemological references.

### *1.4.2.2 Landscape as system*

The vision of landscape as a system of elements connected to each other by energy, matter or information is very close to the vision obtained on adopting the ecosystem approach. But the distinctiveness of the landscape from the ecosystem primarily consists of the geographic context in which the landscape is embedded.

When a landscape is considered as a system, we have to recognize the presence of connected elements creating that system. For instance, such systems can be represented by vegetation patches, geomorphological entities like sand dunes, cliffs, or riparian islands. The relationships between the different parts create a “landscape” system. In the game, we have to introduce the physical properties of the composing elements and their geographical position.

### *1.4.2.3 Landscape as unit*

Defining a unit means that such an entity is distinguished from the background. A landscape is considered a unit if it is possible to delimit borders and assign a distinct function inside either a matrix or a mosaic of distinct landscapes. In such a way, the spatial scale referred to should be large enough to distinguish the units from the surroundings. Units are characterized by autopoietic properties (sensu Maturana 1999). In fact units are closed systems with the capacity to self-regulate and auto-maintain themselves. This assumption seems quite questionable for an entity composed of several items like a landscape, but the self-organization of such a unit is a matter of fact. There are several empirical evidences that are in action inside a landscape (when considered as a unit), including feedback and autocatalytic mechanisms, For instance, the ecotope can be considered as the simplest landscape unit. Ecotope as a functional and independent unit can be structured by natural as well as human processes. An olive orchard could be considered as an example of an ecotope. But by enlarging the spatial scale we can assume, for instance, that the Tuscany landscape is a unit inside the Italian mosaic of landscapes. The unicity of the Tuscany landscape is the result of internal processes based on regional climate, land tenure and cultural processes, and so on, moving across a broad range of spatial scales. Later we will discuss in greater detail the properties of the ecotope.

## 1.5 THE DESCRIPTION OF LANDSCAPE

Landscape can be described either according to an "Ecological" or a "Cognitive" approach. Both perspectives are considered in literature but there is often confusion. We use the term "ecological landscape" meaning between them. While "cognitive landscape" means the subjective reality that surrounds every organism and is strictly related to the autopoietic mechanisms that assure the permanence of self-regulatory and self-maintaining mechanisms both inside and outside the organisms.

### 1.5.1 The "ecological" landscape

We assume that landscape represents the abiotic and biotic context in which the organisms are living. The description of the objects that compose the landscape is carried out simulating a fixed world that could be populated or depopulated by species. On describing the landscape (mosaic) we assume that this mosaic exists for all the species and that the mosaic emergencies are shared by all the organisms according to species-specific censorship. Vegetation cover is the major layout, the template on which other organisms find their "habitat". Several studies in landscape ecology implicitly deal with this approach, in particular from the geographical and land management perspectives.

#### *1.5.1.1 Principles of landscape classification*

It is possible to classify a landscape and the component patches using many approaches that can again be anthropocentric or more independent, according to our perceptive capacity.

Structural patch: generally composed of a soil type overlapped by associations of vegetation.

Functional patch: an area homogeneous for a function or a physical descriptor such as altitude, temperature, moisture and light penetration. In this category we can include the ecotope, a selection of characters which, when they meet together, determine a unique character at a higher level. Ecotope classification is subjective and finalized to a goal. Often the ecotope classification represents an attempt to find a group of spatially coincident characters to correlate with the distribution of a species, of a behavior or, more generally, of a process (see Figure 1.6).

Resource patch; mostly related to the animal ecology, a landscape can be described as a combination of resource patches. These patches are considered part of an animal home range in which food or the nesting site or roosting are easily available and part of the home range in which some specific functions

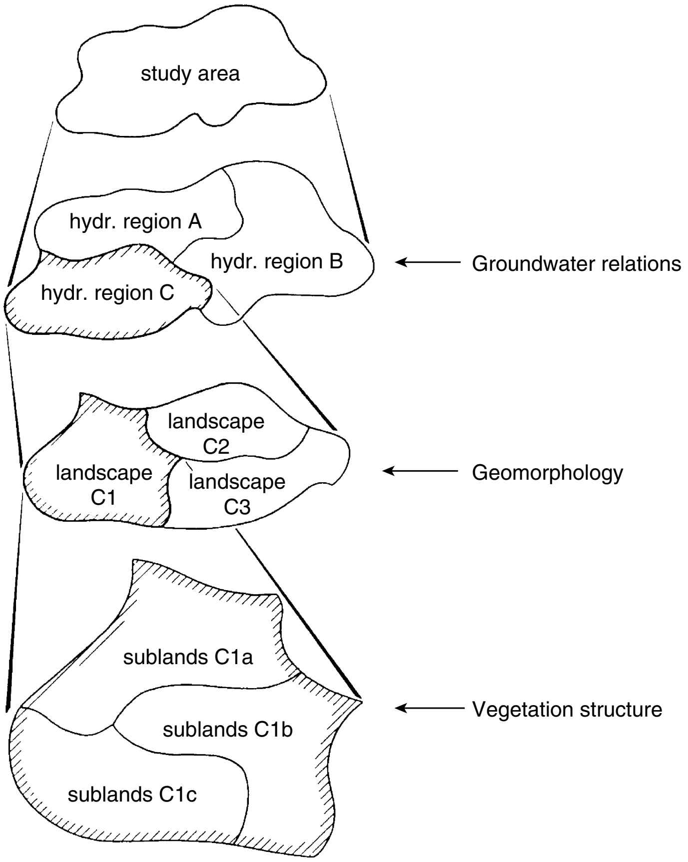


*Figure 1-6.* Example of landscape classification of the Netherlands based on a hierarchy of hydrological regions, geomorphology and vegetation structure (from Canters et al. 1991, with permission).

are concentrated. It affects individuals and is considered equal to or smaller than an individual home range.

Habitat patch : it effects the populations (Ostfeld 1992). May be defined as distinct plant community types that are generally larger than an individual home range. Different groups of organisms can share the same habitat patch.

Corridor patch : although the definition of corridor and their use is controversial, we consider as a corridor patch a portion of the land mosaic that is used by an organism to move, explore, disperse or, migrate. Often, the corridor concept is associated with a narrow strip of land, but for more details see Chapter 4. Generally, we associate corridors with a special feature of an organism that is accomplished outside its "normal" life.

Classification represents a relevant procedure in the study of the land mosaic, especially from the human perspective. In fact, this approach is generally carried out by landscape ecologists interested in studying the interaction between human activity and the landscape. It is particularly useful for the preparation of master plans, to plan natural reserves and in general as competent guidance to many types of land management.

There are no precise classification rules but these change according to purposes, scale of investigation, time and available financial resources. In order to produce a good and useful classification one needs a large amount of information. Main sources are aerial photographs, satellite digital images, cadastral maps, geological, hydrological and soil maps, geographic and bio-thematic maps (vegetation, land use, animal distribution).

All this material should be harmonized and then used differently by *ad hoc* programs and transformed into different types of maps. The first step consists in the creation of physiotopic maps.

A physiotope may be defined as a spatial unit characterized by relatively homogeneous abiotic state factors. Generally, a physiotope is classified using the geology, aspect and slope rate. The physiotope is the basis for further "landscape" classification (Vos & Stortelder 1992). In soil classification, the elementary unit is the pedon and a polypedon is considered as a grouping of contiguous pedons. The bond between different polypedons may be sharp or gradual. The physiotope may be considered a pedon + other edaphic and micro-climatic characters. The ecotopes are the entities created by the addition of vegetation, land use and humus forms and the physiotope. There are no precise rules regarding ecotope classification but approaches vary according to varying purposes and requested details. The classification of elementary landscape units or ecotopes may be comparable to the "site" concept or "facies" (Woodmansee 1990), defined as a biotic community existing in a soil polypedon. The characteristic spatial arrangement of ecotopes create a landscape, but when some ecotopes are found to be more associated than others, it is possible to distinguish land units. A cluster of sites is the higher level of organization that can be compared from microchore to mesochore (Zonneveld 1995). The landscape is composed of site clusters. The higher level is represented by land systems, regions, ecoregions, climatic zones, etc. We can consider this classification as hierarchical: at the lowest level we find the physiotope, although in many cases the physiotope can be larger than the ecotope; then come the ecotope, the land unit and the land system. The ecotope represents the topological dimension of a landscape, while the land unit and higher aggregations represent the chorological dimension.

The ecotope concept can be used with an anthropocentric perspective and bound according to our perceptual capacity. In reality, this concept can be applied more in general to a classification of "landscapes" including plant and animal "landscapes". Although many classifications are proposed (as reported by Naveh & Lieberman 1984; Woodmansee 1992; Zonneveld 1995), we can summarize that classification, in order to be efficient and rigorous, should mention the scale of the hierarchy adopted and the motivations for the choice adopted.

In many human-modified landscapes, the spatial arrangement of vegetation and land uses are so bound by human activity that the land mosaic appears very patchy and the contrast between patches is so high (e.g., old-growth forest bordered by corn fields) that is difficult to imagine a spatial arrangement of the patches in another way. Plants, animals and microbes are forced to live in such types of contrast land.

We have to somehow reduce the importance of classification of the landscape "*per se*" in order to put more emphasis on the processes. Often we do not have enough information about the ecological valence of our *ad hoc* classification of ecotopes. To validate this methodology, we can use biological entities as "eco-indicators". Thus, the Netherlands has been divided into 18 different land units (landscapes) using different combinations of breeding bird species (Kwak & Reyrink 1984). It is the general opinion that landscape classification utilizes different operative scales of resolution according to the purpose and that it is without signification to adopt a standard and rigid classification. For more details on landscape classification see Zonneveld (1995).

The geographic context is also important. For example, the classification of the Apennines or Alpine mountain range landscape is quite different in comparison to the Padanian lowland landscape (Po valley, Northern Italy). In the former case, the topographic complexity creates several climatic, soil and vegetation constraints and completely different habitats are found just a few kilometers apart. In the latter case, we need to travel several kilometers to find the same level of contrast. Again, moving from Padanian valley to the plain of the midwest of the US, we have to travel many kilometers before we find comparable environmental constraint. The advantages of using a classification mainly consists in the possibility of comparing different studies at different sites.

For instance, Meeus (1995) suggests 30 categories of landscape according to multiple criteria in which morphology, climate and land use create distinct units (Figure 1.7).

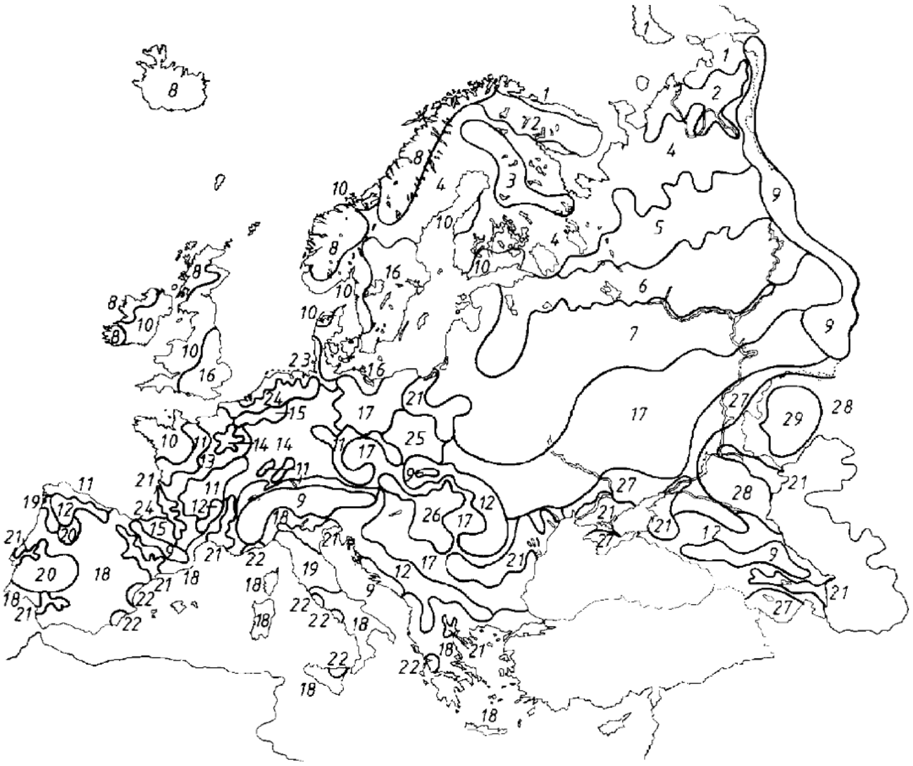


*Figure 1-7.* Distribution of pan-European landscape types (from Meeus 1995, with permission).

1. Artic tundra
2. Forest tundra
3. Boreal swamp
4. Northern taiga
5. Central taiga
6. Southern taiga
7. Subtaiga
8. Nordic highlands
9. Mountains
10. Atlantic bocage
11. Atlantic semi-bocage
12. Mediterranean semi-bocage
13. Atlantic open fields
14. Continental open fields
15. Aquitaine open fields
16. Former open fields
17. Colletive open fields
18. Mediterranean open land
19. Cultura promiscua
20. Montados/Dehesa
21. Delta
22. Huerta
23. Polder
24. Kampen
25. Poland's strip fields
26. Puszta
27. Steppe
28. Semi-desert
29. Sandy-desert
30. Terraces

The apparent anthropocentric classification adopted by different authors at the human scale can be easily converted when the landscape concept is used to describe vegetation and animal patterns. Instead of "dogmatic" conflicts in landscape ecology we often find many convergences.

The hierarchy in anthropocentric landscape classification (ecotope, micro-, meso-, macro- and megachore) is finalized to describe the different processes that have some interest to people and they are comparable to the administrative organization of a region. An olive orchard may be considered as an ecotope, and the combination of olive orchard + alfa alfa field + woodlot may be considered a microchore (land facet), which corresponds to a farm in the Northern Apennines (Italy). A sequence of farms of this type, the so-called *cultura mista appenninica* composes a mesochores (land system) that could represent a parish. The combination of mesochores creates a landscape (macrochore).

This classification is functional for human use and has a relevant ecological meaning, offering a lot of information for applications. These four levels of land classification link human socio-economic structure to environmental resource allocation. However, this model works well in a rural perspective; moving to urban and industrial landscapes the hierarchical factors change, losing the "ecological" (*sensu stricto*) feedback.

The information enclosed in this adopted classification can be measured using the species diversity *sensu* (Whittaker 1977). The alfa diversity can measure the microchore complexity, the beta diversity the mesochore, the gamma diversity the macrochore, the delta diversity measures the complexity of a region and, finally, the regional (epsilon) diversity measures the complexity among regions (Naveh 1994).

An example of levels and types of species diversity is presented by Wiens (1989). This author has measured the diversity of birds according to different area aggregation. It is clear that these choices are arbitrary and depend on the goal of the study, but it is universally accepted that different levels of the ecological hierarchy possess different information.

### 1.5.2 The cognitive landscape

Most of the actual studies on landscape are based on the description of patterns and processes that human bio and remote (extra-soma) sensings are able to perceive. Often we use some paradigms to describe distinct features that are transformed into maps or numerical shapes in a second.

If we pose a biological entity at the center of the "real world", the perceived surrounding is the world of such an organism. Von Uexküll (1940) firstly described this "subjective world" as "Umwelt". According to this vision, an organism could perceive three types of surroundings that we call, respectively, Neutrality-Based Landscape (NBL), Individually-Based Landscape (IBL), and Observer-Based Landscape (OBL) (Farina et al. 2004) (Figure 1.8).

The Neutrality-Based Landscape can be considered a indistinct part of the perception, the noise background that is not transformed into signs by the sensors. For instance, when we are in a noisy bar we cannot distinguish the words of individuals but sample a mix of vocalizations. In the same way, looking from the top of a mountain we observe the surroundings without concentrating our attention on a specific object. The NBL can be considered the uncoded part of the signals uttered by the surrounding entities.

The Individually-Based Landscape is part of surroundings that organisms decodify using somatic sensors and that incorporate cognitive mechanisms. Evolutionary adaptative mechanisms are implicated in this process and are driven by genetic processes. Later, we will discuss in greater detail this perceptive mode that represents the main link between the external and the internal world of every organism.

Finally, the Observer-Based Landscape is the piece of real world perceived by people by using a cultural filter. This vision is not incorporated into the genetic makeup but experience and learning are stocked into a temporary memory that do not survive the organism's death. Cultural mechanisms have to be invoked. Considering the dramatic explosion of human cultures, it is easy to predict the complexity and the broadness of the OBL. The OBL changes according to our background culture and our personal experience (see i.e. Eisler et al. 2003). The OBL pertains mainly to humans but it could also be extended to many other organisms when experience is used to modify

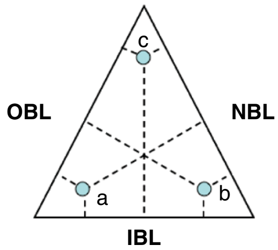


*Figure 1-8.* Ordination of human landscape closure (HLC) (OBL: Observer-Based Landscape; NBL: Neutrality-Based Landscape; IBL: Individually-Based Landscape) according to the three main patterns of socio-economic development. (a) Modern people with low culture and high technological confidence; (b) Modern people with high culture and technological confidence; (c) Primitive people with no written culture and little technological confidence but with a high cognitive capacity (from Farina 2004, with permission).

the innate behavior. For instance, a trained horse has a larger range of recognized human signals than a wild horse. An aged fox has a higher ability to find prey than a young individual, etc. We call the human landscape closure (HLC) the relationship among the three different human perceptions of the surrounding. Every man perceives the surroundings based on the three possibilities (see also Ohta 2001). The ascribtion of functional attributes to structural landscape features such as patches and border is not automatic but requires information as to how organisms perceive and react to landscape structure (Collinge & Palmer 2002).

A further classification can be made assuming that man, plants and animals have a different perception of the surroundings. Starting from this perspective we can order our interest in landscape processes according to one of the three subjects: plants, animals and man. But a further distinction could be done for viruses, bacteria, fungi, algae and protozoa.

The geobotanical perspective: The distribution in the space of abiotic and biotic components of the environment, from the soil landscape to the landscape "perceived" by plants, and to the distribution of plant entities as communities, woodland, prairies, timber lot, etc. For plants, the perception has to be considered in a broad sense as the range of "sensitivity" of the plant life's requirements and its capacity to incorporate information from the neighboring environment. This is in direct connection with the breadth of adaptation, colonization and survival to natural and human related stress.

The animal perspective: As animals perceive landscape. This perspective is conceptually related to the human perceived landscape, although a substantial difference exists: In the first case, the scale at which the landscape is studied is a human scale. In the last case, the whole approach is scaled on direct or predictable animal species-specific scales (Figure 1.9).

The human perspective: as a human perceives the landscape. In the human perspective, landscape is desegregated and grouped again according to functional entities that have a meaning for human life. The human perspective includes perception, values and culture, all strictly connected by bio-semiotic processes (Nassauer 1995).

The three approaches are not in contrast to each other, but each explores a dominion of patterns and processes that, in the last analysis, are components of the whole complex biological and ecological system.

There are more commonalities than differences in the three approaches like space and the spatial arrangement of processes and patterns. Additionally, although it does not always emerge explicitly from the studies and research in landscape ecology, landscape ecologists are really aware of the strict interactions between the human world and nature, and also of the strict interdependence of the systems. The exigence to place in real space at the right scale a pattern or a process is a common goal of landscape ecologists.

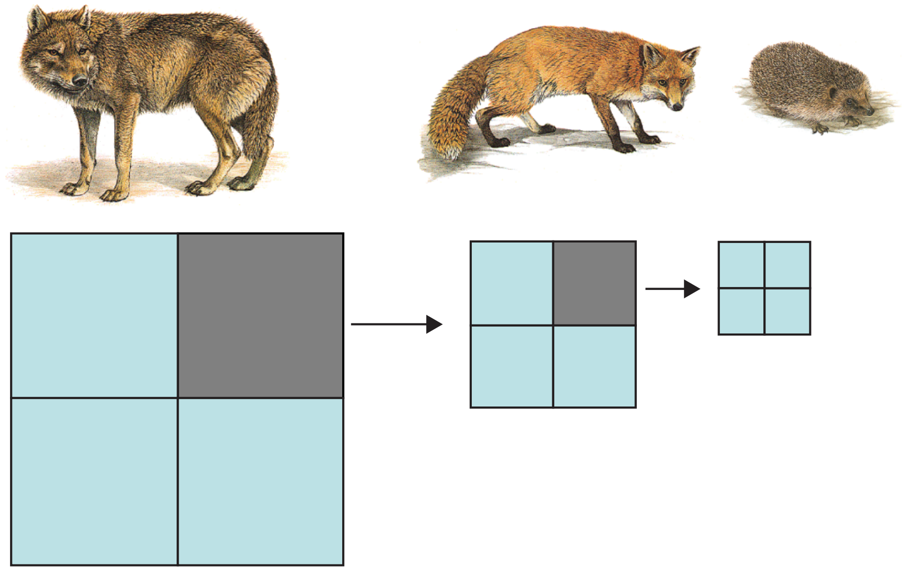


*Figure 1-9.* Three examples of organism-centered landscapes : (a) Hedgehog (*Erinaceus europaeus*), (b)Fox (*Vulpes vulpes*), (c)Wolf (*Canis lupus*). Grain and extent appear species-specific. In the Northern Apennines the hedgehog landscape is represented by prairies and shrubs bordered by woods (the size of area is approximately 300 x 300 m). The fox landscape is represented by prairies, fields and dense and open woodlands (the size of the area is approximately 3 x 3 km). The wolf landscape embraces a catena range and is represented by prairies and pastures, woodlands of different types, clearing and edges (the size of the living area is approximately more than 10 x 10 km).

Today, these three approaches have a common theoretical basis as described previously, considering the landscape as a domain, a unit or a system. The cognitive landscape closure (NBL, IBL, OBL) can be differently applied to animals, plants and humans. Every form of life has cognition: cognition is life—and every organism has autopoietic characters that create either a separation between the internal world from the external (see for more details Maturana & Varela 1980), or a continuity.

The human dimension of landscape is probably the more intriguing approach due to the overlap and the strict interweave of biological and cultural components of humanity. This dimension is related to processes having a broad temporal and spatial scale. The "biological" dimension of humans may be compared with that of animals, but the cultural component of humanity is unique and this is the more interactive component with the environment, especially because of the dominant attitude of human culture and the practical capacity, using technology to bypass natural and ecological constraints and limitations. From the three perspectives the challenge to combine theories, paradigms and models produced by the traditional "mono-disciplinary" approaches is evident and is the leitmotif.

The complexity of the environment is so high that this approach is also just an attempt to gain a partial understanding. Landscape ecology does not have the capacity to explain all the processes but can undoubtedly understand the complexity better than other ecologies, that means the interrelationships among different processes and patterns.

The common denominator is the spatial dimension of the processes and their importance for other spatial and non-spatial processes and the neighboring characters are one of the relevant foci of landscape ecology.

The main strength of landscape ecology consists in the capacity to transfer information across different families of processes that occur at different spatial and temporal scales.

The risk of considering landscape ecology from an exclusively anthropocentric point of view is very high at the moment, and this could produce a dogmatic discipline deprived of theoretical and experimental verifications. On the other hand, a landscape ecology science simplified as "ecology at a broad scale" is an unacceptable and reductive view of the landscape ecology.

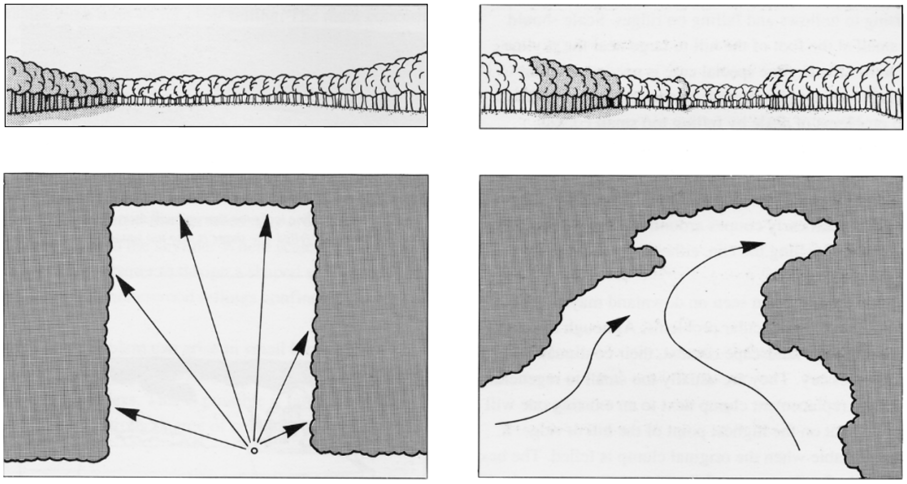
The spatial dimension of the ecological processes has been recognized as extremely important to progress from an ecosystemic topological vision of ecological functioning to a chorological approach in which the real world is studied.

A human landscape, a plant landscape and animal landscape, all compose the environment of the planet and land-scape, sea-scape or water-scape, more in general, air-scape are the context in which ecological processes are acting. This premise is extremely important to understand the choice of arguments and their position in this book. Landscape ecology may be considered a new science, especially for people addressing the human perspective, or it may be considered a pioneering approach of ecology if geobotanical and animal perspectives are selected. In the first case, the study of human-related processes accompanied by processes created by other abiotic or biotic entities (plants, microbes, animals) there originates a more sophisticate pseudo-virtual context greatly appreciated by scientists working in disciplines like anthropology, sociology environmental psychology and architecture.

The human and animal perspectives have some common points when the scale of perception of the animals is close to the human one. In this case all "benefits" gained by humans in shaping and/or controlling landscapes are shared by some groups of animals.

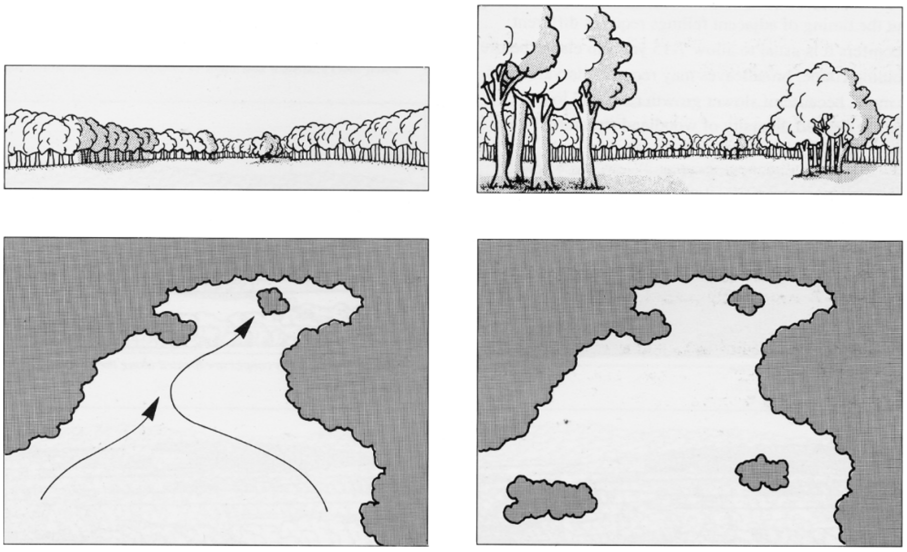
Landscape design carried out by experienced architects can change the availability of resources to favor, for instance, some mammals and birds. In Figure 1.10 is an example of how to create more complexity and edges in a

59. The designs of feeling areas in flat landscapes.



a. Rectangular space - the eye roams aimlessly seeking interest which is not present

b. Shaped space - the eye is drawn through the space winding from side to side



c. Shaped edges drawing the eye through the space to feature

d. Foreground retentions give a sense of depth

*Figure 1-10.* Structuring the landscape consists not only in changing the scenery value but also create or vanish structures with spatial and ecological attributes. In this case the activity was devoted to increase the spatial complexity of a clearing (from the UK, Forestry Commission 1991, with permission).

restored rural landscape in the UK (Forestry Commission 1991). Many scenic landscapes are very attractive for tourists as well for wildlife (see Schmid 2001). Some caution should be introduced about this approach that exceeds ecological criteria and models. In fact, here the benefits are shared between humans and animals are adapted to live with humans but by reducing the survival chances for "more exigent" species.

But when the restoration or the mitigation of a degraded condition created by human activity in a pristine environment like the old-growth forest of the Pacific USA are requested, this approach is clearly insufficient and dangerous. For some species such as large carnivores or for nocturnal raptors like the spotted owl or for most of the neotropical birds that use the landscape in a very complex way, we need more information and a landscape planning that, at first sight, is not coincident with human common sense. In this case, we need deep ecological background and strong models working in an explicit way, rather than considering physical and biological components. There is also another limit in this approach that without population dynamic knowledge spanning the life-cycle of a species we could create unintentional sink habitats, accelerating a gradual decline in the "target" organisms.

To improve the human-related approach without doubt a strong interaction is necessary between geobotanical and animal perspective that can be incorporated into the common practice of this anthropocentric approach. It could be extremely important to predict the survival chances of many species and entire ecosystems. Figure 1.11 reports the scenario of private versus public cutting of forest landscape in Oregon between 1972 and 1988 (Spies et al. 1994). Private cutting has produced a dramatic decline of the pine forest due to unselected cutting; the public forests have been fragmented but the pine matrix survives.

### *1.5.2.1 Spacing: The perception of the landscape*

In this section, we will describe relevant elements linked to the perception of surroundings like space, embodiment, safety, aesthetic, amenity, scenery, etc., that represent a miscellanea of arguments that have the cognitive process in common. This is a very promising field in which to develop landscape ecology.

Space may be considered as "The final frontier for ecological theory" (Kareiva 1994). We refer to "spacing" as the attitude of an organism reacting to the perception of the neighboring environment (the landscape).

The spacing or spatial arrangement is a scaled property of living organisms, from individuals to populations, communities and metacommunities. Organisms react to external stimuli integrated by internal biological demand so as to optimize resources and energy to provide such resources. Spacing is the ecological reaction of organisms to a nonuniform distribution of resources (habitat suitability) and to intra- and interspecific competition in space and time.

This concept is central in landscape ecology; see also the chapters devoted to heterogeneity, fragmentation, metapopulation, etc. Grain is the minimum

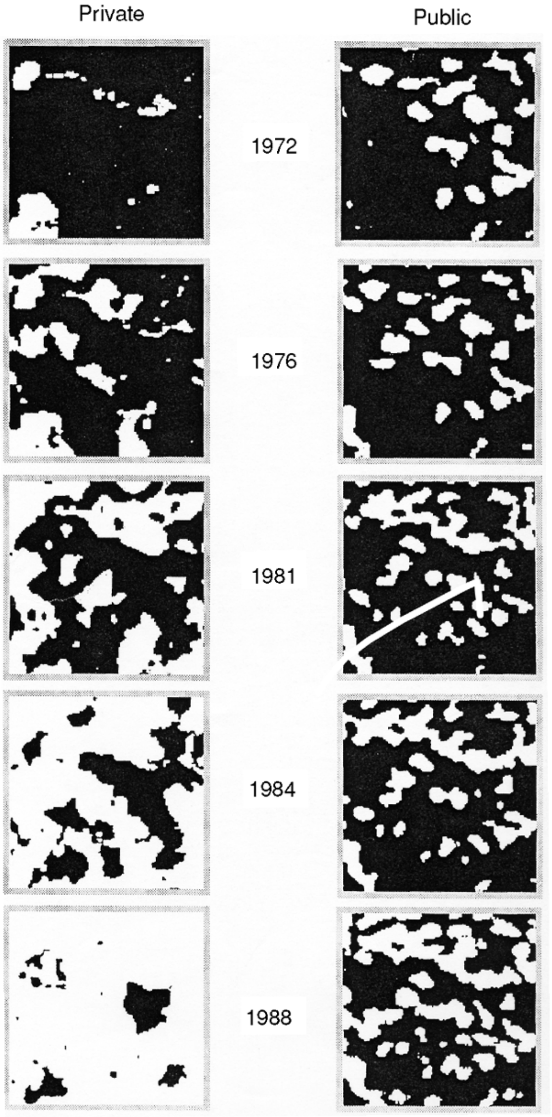


*Figure 1-11.* In Oregon, forested landscape changes according to private and public ownership type. In black are indicated conifer types; in white other types of woodland (from Spies et al. 1994, with permission).

area at which an organism perceives and responds to the patch structure of a landscape (Kotliar & Wiens 1990).

Extent is the coarsest scale of spatial heterogeneity at which organisms react. The response of a biological entity to the different availability of patch habitat will be considered across different spatial and temporal scales. Pearson

(1991), conducting experiments on the foraging pattern of field sparrows and white-throated sparrows, described the different spatial arrangement of individuals foraging in a cage. In field sparrows, individuals birds were feeding close to each other, but with white-throated sparrows, individuals used the entire available space, avoiding violation of individual distance (Figure 1.12).

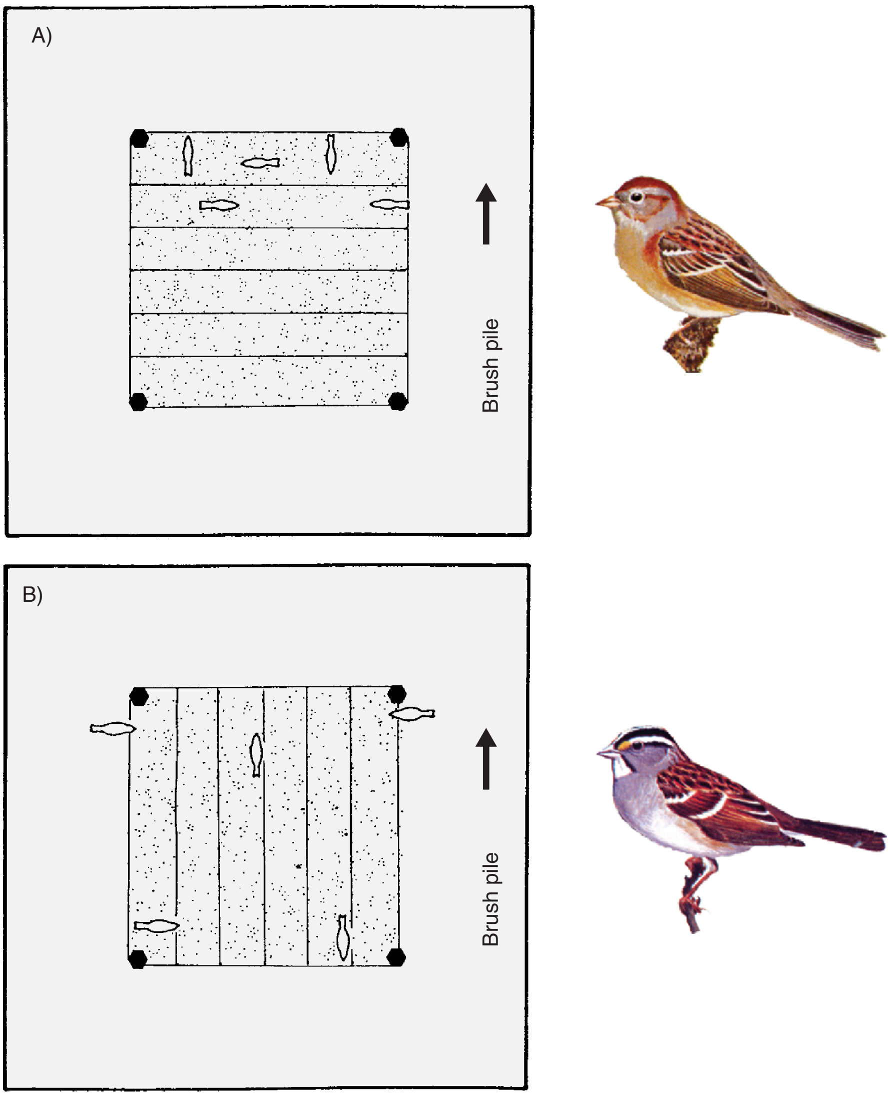


*Figure 1-12*. Field sparrow *Spizella pusilla* individuals can forage close to each other, while white-throated sparrow *Zonotrichia albicollis* maintain a high inter-individual distance during their food search path, from an experiment of Pearson (modified from Pearson 1991, with permission).

This behavior can be better appreciated in populations of frugivorous birds in winter time. During the warmer days, flocks are relaxed and species are dispersed in the environment. But when the temperature drops the inter-individual distance is immediately reduced and species can co-exist close to each other in areas where resources are still available. Thus, in conclusion, spacing is not determined only by external cues and habitat availability but also by physiological constraints, and this creates a more complicated scenario to investigate. Spacing depends mainly on resource availability.

Plants react to resource availability arranged in a finite and predictable pattern. The African acacia savanna is a typical example. In Europe, this patterning is represented by the Spanish “Dehesa” and by and Portuguese “Montado” (Figure 1.13) .

Animals have a great sensibility to the surroundings especially when anti-predatory behavior, intraspecific competition, or homing are performed. There are species that forage separately and show strong territorial behavior. One example is represented by the European robin (*Erithacus rubecula*). This species patrols an area, fighting any other individual that does not respect the ownership. The defended patch, in many cases, is composed of not only a

*Figure 1-13.* The Spanish Dehesa (Montado in Portugal) is a man-made savanna in which the plant spatial arrangement captures the soil water availability.

mosaic of fields, hedgerows, woodlots of different extension according to the territory patch quality, but also by the competition pressure, abundance of other individuals, and, finally, by the attractiveness of the area at a larger scale (Farina 1993).

Public information is a mechanism for learning from the behavior of other intra or inter-specific individuals about resource quality and availability. Public information is collected using visual or acoustic cues uttered by other individuals. This mechanism can change the evaluation of the patch selection independently by the structural composition of the patch and forces us to reconsider the role of the geo-botanical or land-use landscape in patch occupancy and use (see Smith et al. 2001).

### *1.5.2.2 Space and memory*

The episodic memory refers to the ability to encode and recall unique, past experiences. Some birds like tits and jays have the capacity to recover the food stored in holes or in other temporary refuges after some time. This capacity requires a cognitive map of the surroundings. This memory, localized in the mammal hippocampus, allows individuals to provide information about the "what" and "when" events ( Griffiths et al. 1999; Griffiths & Clayton 2001). The study of this memory could open new perspectives to better understand the "cognitive landscape" in non-human animals.

Learning and remembering of spatial patterns has been demonstrated in different groups of animals like humming birds (Sutherland & Gass 1995) and sheep (Dumont & Peptit 1998; Dumont & Hill 2001) living in an heterogeneous environment. Cognitive maps in birds have been localized in the hippocampus and play a critical role in some aspects of map learning (Bingman & Able 2002).

### *1.5.2.3 Embodiment and cognition*

Embodiment refers to the role of the body in cognitive processes. Embodiment requires structural coupling between the system and the environment (Riegler 2002). There are two different senses of embodiment: the state of being embodied and the act of embodying. The act of embodying assumes that the body changes with time according to functions and states. Affordance refers to the opportunities for action that objects, events and places provide for animals. The opposite is represented by the effectivities that are the act an animal uses to realize a specific affordance. Effectivities change according to the status of the animal, because these are the properties of the animal. Tools like a stick or a microscope, extend the effectivities and this capacity increases the possibility of humans to make use of more affordances than other animals (see also the concept of niche construction). Spatial cognitive maps are tools that extend the environmental affordance. The capacity to attach tools to the body means that the body does not have a boundary that is fixed at the surface of the skin but can be extended beyond the skin (Hirose 2002). Appendages like vibrissae and tools represent ways to increase the perception of the surroundings and, finally, the property of the environment can be perceived by non-neural extension. Affordance depends on the scaling property of the body. This is necessary to introduce an intrinsic metric to calibrate such affordances in species-specific terms (Figure 1.14).

The traditional organism-environment dichotomy is revisited in terms of complementary in which organismic behavior and the effects of the environment are part of the same organismic world and behavioral functions seem to maintain perceptual homeostasis (see Weems 1999). This last concept means that organisms react to changing patterns according to the appearance of a gradient that could be a variation in electromagnetic waves as well as a change in surrounding organisms. When the anxiety in children reaches levels of pathology, it could mean that an affordance for safety is not perceived. This does not explain the causes of the anxiety but explains the mechanisms of anxiety control. The potential for understanding behavior with a construct that cuts across the traditional organisms-environment dichotomy, is encouraging, says Weems (1999). This is extremely important in developing a robust theory of organismic-centered landscape.

### *1.5.2.4 Safety and aesthetic landscape, amenity*

The aesthetics in landscapes is decreasing at alarming rate world wide and the causes can be found in urban development, agriculture intensification and changes in land use. These causes have an objective explanation, but if we question why the aesthetic value of landscape has not been carefully considered by society as a value to be conserved like a painting in a museum, we do not have a valid explanation. A hypothesis consistent with the theory of ecological psychology could invoke a safety affordance in past landscapes. People in the past were completely dependent on landscape resources; today, society depends on fossil fuels and other sophisticated energies. The maintenance of landscape configuration was essential and the sense of beauty was coincident with the sense of safety, victory and success. Today, we seek these values in other domains outside the landscape, like on the web net, or in the completely engineered environment of cities. Today, safety affordance is searched for in other places. If we associate beauty to the optimization of system functionality, we can say that cultural landscapes are the result of such functional performance produced by human intervention (see Ewald 2001). In

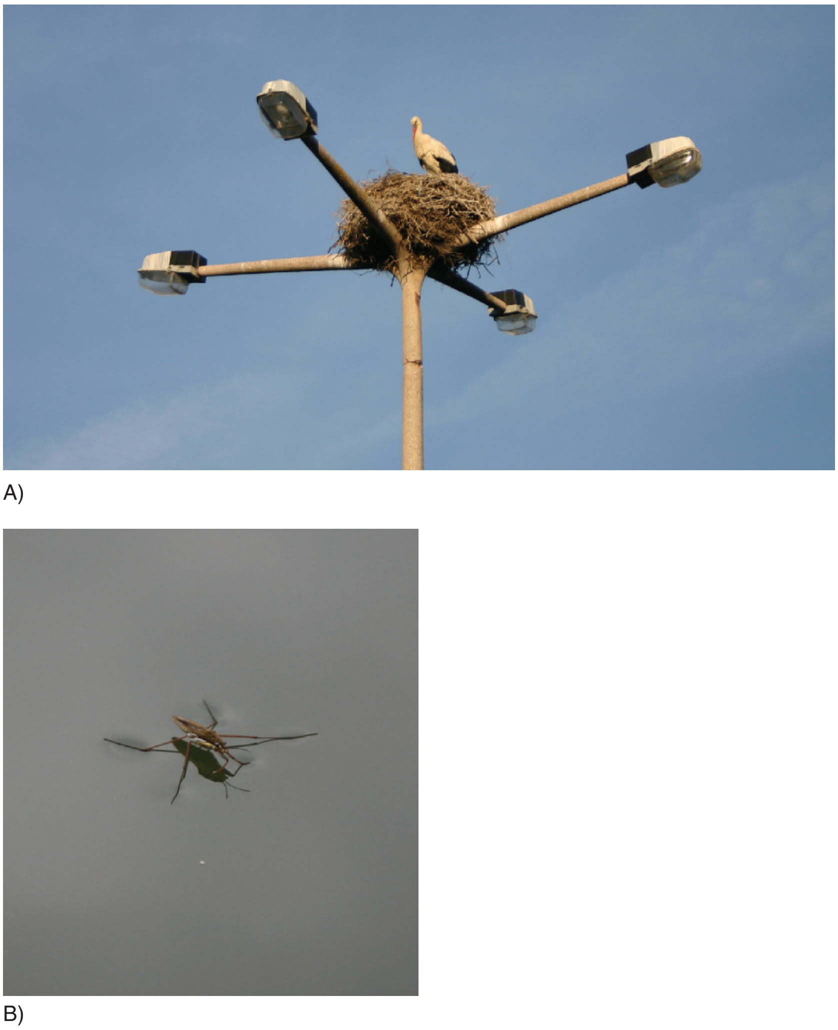


*Figure 1-14.* Affordance means the interaction between organism and its surroundings. In case A, stork (*Ciconia ciconia*) uses a urban lamp as a support to nest. In case B, a pond skater (*Gerris sp.*) uses the surface water tension as terrestrial mammals use the ground. Every object has a different affordance according to the organisms that enter into contact with it.

the present-day culture, beauty and efficiency are not explicitly connected and we have to move via *ad hoc* paradigms to connect the two aspects. A beautiful landscape is necessary for urban-centered human perception; there is a further semiotic step between.

The aesthetic is a relevant resource of landscape for local populations as well for tourists. In regions like Switzerland, the aesthetic is maintained by traditional agriculture and represents an additional land value ( Schüpbach 2003).

Aesthetics can meet a multifunctional goal when coupled with other ecological functions. For instance, the ecological functions of woodland edges such as habitat, refuge, corridors and buffers can play the role of amenity resources (historical, symbolic and aesthetic qualities, wildlife experience, berry and mushroom picking, hunting, hiking, etc.) (Fry & Sarlöv-Herlin 1997). But the aesthetic represents an economic value in the real estate cycle (Bourassa et al. 2003). In particular, three aesthetic externalities (the presence of a water view, the appearance of nearby improvement, and the quality of landscaping in the neighborhood) are important in residential property markets although, as argued by these authors, the value of an aesthetic resource largely depends on local abundance.

### 1.5.2.5 Topographic prominence, the visual landscape

We can define topographic prominence as the height differential between an individual and his/her surroundings as apprehended from the individual's point of view (Llobera 2001). It is the perception of terrain that lies below the individual's location (Figure 1.15). Topographic prominence must have been very important during prehistoric times when human affordance was strategic for survival. Hunters or defenders probably used the topographic heterogeneity of the land to increase the specific performances. According to the differ-

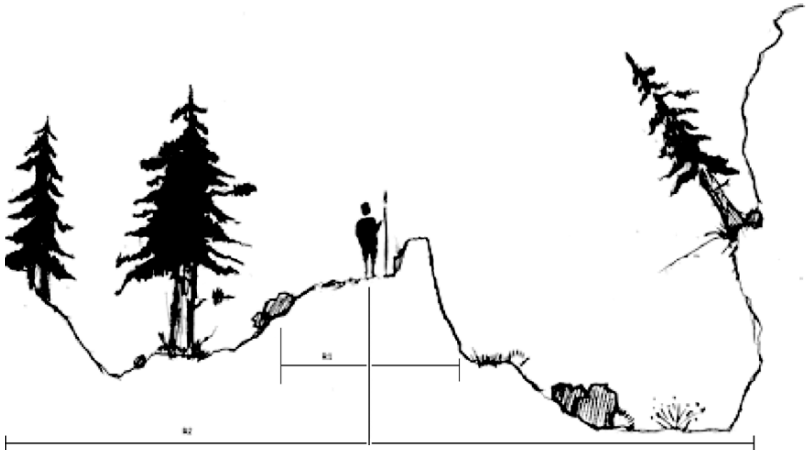


*Figure 1-15.* Change of topographic prominence with scale (from Llobera 2001, with permission).

ent uses, prominence is changed scalarly. If a small radius is used, prominence assumes high values, but such values decrease dramatically when the radius is enlarged. Often we appreciate the shape and scenery of the visible landscape but we do not pay attention to the visible and invisible part of the territory when we move across and can or cannot observe details (Krause 2001; Baldwin et al. 1996) or underestimate the importance of the visual complexity of the landscape and species diversity (Hehl-Lange 2001).

### *1.5.2.6 The psychological landscape*

This is a new field of investigation in which human decisions (behavior) are analysed with specific reference to psychological drivers (Kaplan & Kaplan 1989). Environmental attitude and ecological behavior are two components of the human decision (Kaiser et al. 1999) and ontogenesis (Kytta 2002). The analysis of the psychological reactions can improve the knowledge of landscape evaluation and the successive actions (planning, conservation) (Bell 2001).

### *1.5.2.7 Mystery in landscape*

Mystery is defined as the degree to which you can gain more information by proceeding further into the scene (Kaplan & Kaplan 1982). Mystery is one of the perceived attributes of a human-centered vision of landscape. The perception of mystery decreases with perceived distance. The perception of mystery declines correspondingly with perceived screening. The perception of mystery increases with the increase of spatial definition and the perceived physical access (Lynch & Gimblett 1992).

### *1.5.2.8 Behavioral ecology and landscape ecology*

Among the several topics considered by behavioral ecology, like animal decision making for movement, dispersal and habitat selection that determine their dynamics and spatial distribution, many are common to landscape ecology (Gagliardo et al. 2001).

Unfortunately, few contacts are at present established, especially between the two research fields due to difficulties in finding a common scale of interaction (Lima & Zollner 1996; Bennet 1996).

Perceptual range is defined as the distance from which a particular landscape element can be perceived. This represents the “species-specific window” of identification of the “greater landscape”.

This property plays a fundamental role in the survival of individuals. A species that has a low perceptual range can expect a high risk of mortality, spending more time to search for an available habitat compared to a species that has a high perceptual range. In case of habitat heterogeneity and low perceptual range, a species can experience a high risk of predation.

Using a metabolic ecology approach, Jetz et al. (2004) have demonstrated the importance of behavior, body size and home range in mammals. It remains to be investigated at what scaling a neighbor is detected.

Other mechanisms can be used by organisms in selecting suitable patches. For instance, Reed & Dobson (1993) have considered the role of conspecific attraction in habitat selection. The presence of individuals in a patch can be an attractor for other conspecifics, and it is often possible to observe a higher density despite resources that do not deviate from empty patches. Often, empty patches remain in such a status of lacking conspecific attractors. This has important implications in conservation strategies like the reintroduction of an extinct species. The lack of conspecific attraction in a suitable patch can depress dramatically the survival of the reintroduced individuals, which cannot use the experience of local populations.

On the other hand, Pierce et al. (2000) have excluded land-tenure and prey partitioning from the factors that regulate abundance and distribution of mountain lions (*Puma concolor*). They argued that mountain lions are distributed according to prey availability and that territorial overlap is reduced by reciprocal avoidance. Probably, other mechanisms are working in the complex interactions between mountain lions and mule deer (*Odocoileus hemionus*), which are not mediated by landscape patterns or behavioral mechanisms.

The perception of landscape patchiness is fundamental to animals. For instance, the foraging activity of big horn sheep (*Ovis canadensis*) in a heterogeneous landscape has been explained by Gross et al. (1995) by the application of a nearest-neighbor rule. Some species like birds probably have a great perceptual range, especially in some seasons. Chemical signals could improve this capacity in many arthropoda, and honey bees can have a better orientation when the landscape is in topographic irregularities (Southwick & Buchmann 1995).

Patch selection and movements are also largely dependent on the conspecific attraction. An individual tends to settle in a patch occupied by other conspecific species (Smith & Peacock 1990, for a review).

At the landscape level, animals tend to concentrate in some patches and the dispersion is a real deterministic process. This is well documented for birds outside the breeding season either during foraging or roosting behavior.

The perception of corridors is another focal point under discussion. Some species use corridors extensively that have recognizable structures like hedgerows, but in many cases corridors are perceived by animals through a species-specific integration of visual, acoustic and scent cues. By using spatially explicit models and the source-sink principle, we can assume that animals select the more suitable patches among the ones available in the landscape. Animal movement and patch selection are determined by many internal and external cues using spatial memory, cognitive maps and conspecific attraction. A new, unexplored opportunity to understand the perceiving capacity of animals is determined by the human-altered landscapes in which animals have to face new landscape configurations, in many cases representing true novelties and different from the one in which they evolved. For instance, forest animals are now living in a more fragmented landscape and their "maladaptation" (see Blondel et al. 1992) to the new patterns can be used as a tool to investigate the evolutive processes.

The use of behavioral traits like biomarkers could introduce new perspectives in the investigation of the effects of landscape structure on species. This technique has been utilized by Lens et al. (2002) to evaluate avian persistence in fragmented rainforest in southeast Kenya. They used the fluctuating asymmetry and mobility as indicators of the effects of fragmentation on selected species. The Fluctuating Asymmetry (FA) was measured in tarsus length. Small nondirectional differences in the development of the left and right side of bilateral traits are considered to be an indicator of developmental stability of a population in a specific habitat. Fluctuating Asymmetry was found to be correlated to forest deterioration due to fragmentation. The comparison of FA from museum samples of birds living at the time of continuous forest confirmed the hypothesis of the effect of habitat fragmentation and change in a secondary life trait.

### *1.5.2.9 Information landscape*

Information landscape represents the mosaic built by information that an individual can perceive. It could be considered quite different from the cognitive landscape that represents the landscape created by the mind. Information landscape and cognitive landscape, when fitted, are the expression of the eco-field. Information landscape hypothesis can be used to explain the distribution pattern of foraging activity in birds. Some evidence on tits (Naef-Daenzer 2000) demonstrates that the use of resources is preceded by a general survey of searching for food. Individuals start to exploit the nearest tree around the nest, and moving far, according to the reduction of prey availability (Figure 1.16).

In honeybees, the retinal image flow represents the perceived surroundings. Experiments carried out by Esch et al. (2001) clarify the mechanisms of surroundings perception in this species. The landscape grain, experimentally varied by using a black-white mosaic, seems to be the key cue used by bees to store information and distance on the surroundings.

The fact that an ontogenetic learning mechanism is adopted by honeybees has been also observed using an harmonic radar. At the first experience outside

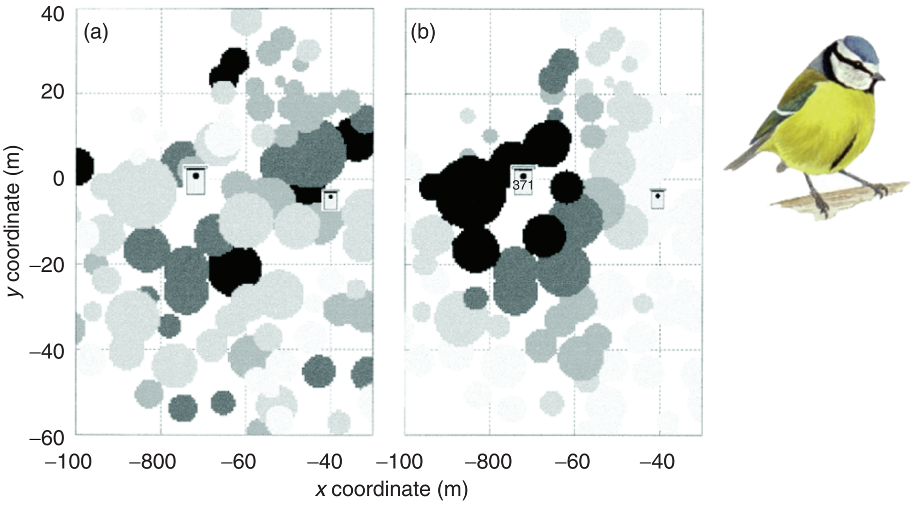


*Figure 1-16.* Distribution of prey availability (a) and location density of radio tracked tits (b) aroud the the next (#371). The circles represent the trees diameter and the color from gray to black, high prey density and radio locations, respectively (from Naef-Daenzer 2000, with permission).

the hive, individuals perform short exploration flights, but a few days are sufficient to train the individual to be accustomed to the surroundings (Capaldi et al. 2000) (see Figure 1.17).

### *1.5.2.10 The eco-field hypothesis*

Recently, Farina (2000, 2001, 2004) and Farina & Belgrano (2004), in order to connect the niche theory (Grinnell 1917, Hutchinson 1957) with the habitat paradigm and the spatial attributes of the perceived landscape, described a new cognitive paradigm called "eco-field".

Adopting the vision of the "subjective surrounding" or Umwelt of the von Uexküll school (von Uexküll 1940 (1982)), the eco-field is defined as the "space configuration meaning carrier" under the epistemological umbrella of the Individually-Based Landscape (IBL).

According to this paradigm, every function that a species activates needs a specific spatial configuration recognized by innate cognitive mechanisms (Figure 1.18). A species settles where such a configuration exists. The life-cycle of every species is composed by the temporary activation of life functions like foraging, resting, mating, drinking, orienting, patrolling, etc. Every function requires a specific spatial configuration of objects that in some cases are

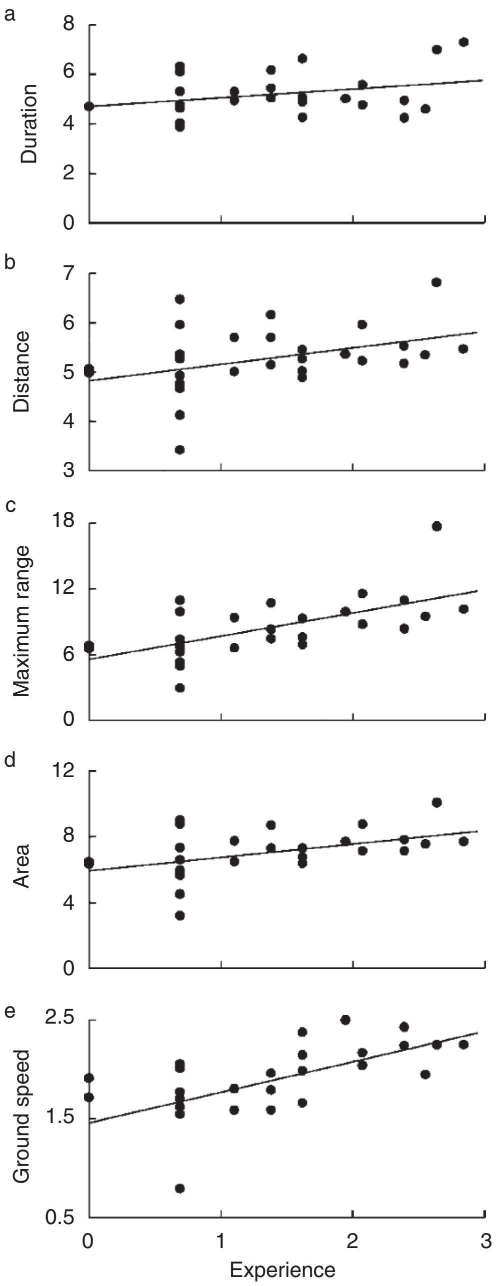


*Figure 1-17.* Correlation between flight experience and environmental effectivities in honeybees revealed by harmonic radar (from Capaldi et al. 2000, with permission).

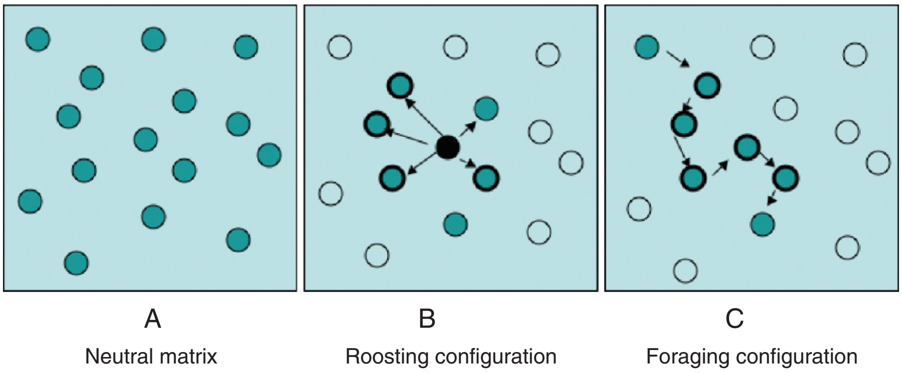


*Figure 1-18.* Into a neutral matrix every species can recognize a *spatial configuration* meaning carrier according to the life function that it needs. In this example, the neutral matrix is represented by trees (A). To roost, the organism requires the configuration (B), while for foraging, plants must have the configuration (C). If the neutral matrix has such potential configurations, the matrix becomes the habitat for that species. Plants with a thin margin are used for only one of the two functions.

recognized by a comparison with a cognitive map as described in animal navigation (Gallistel & Cramer 1996; Dyer 1998). Animals have cognitive capacities to assure a spatial memory (see Dyer 1996 for the honeybee and Tammero & Dickinson 2002 for Drosophyla) or an olfactory memory, like in crickets (Matsumoto & Mizunami 2002) or in honeybees (Thorn & Smith 1997), in food-storing birds (Sherry, 1989; Sherry & Duff 1996; Kamil & Chemg 2001), in searching for food by ants (Graham et al. 2004), and in reorienting in fishes (Sovrano et al. 2002). Spatial learning has been found to be correlated with sexually dimorphic status in meadow voles (*Microtus pennsylvanicus*) and deer mice (*Peromyscus maniculatus*) (Galea et al. 1996), where gonadal hormones are responsible for differentiating the spatial performance. Changes in behavior and spacing occupation have been observed in male robins (*Erithacus rubecula*) (Tobias & Seddon 2000), supporting the hypothesis that changes in function (modulated by a change in physiological status) elicit a different surrounding appreciation. Age is an important variable in this case. For instance, Robichaud et al. (2002) have found a different perception between juvenile and adult birds dispersing along a riparian buffer strip surrounded by a managed forest.

Displaced pigeons extensively use familiar landscape and this improves homing capacity, as discussed by Wallraff et al. (1999) and Biro et al. (2002). Pigeons released after 5 minutes of preview of the surroundings have a better homing performance compared with individuals released immediately.

For instance, a skylark (*Alauda arvensis*) searches for seeds to eat; the seeds can be found in several environmental contexts from woodland clearings to open prairies, but it is only in prairies that skylarks live. This means that every function requires a searching image fixed mostly by adaptive mechanisms expressed by genes. We have no idea as to how the specific functions switch on the neural system searching image necessary to satisfy the expressed need. If, for every function there exists a space configuration, meaning carrier, the habitat for a species is determined by the summation of all the eco-fields. Moreover the eco-field is the combination of natural objects necessary to process a specific life function. For individual survival, a species requires several eco-fields that in general exist in the same geographical space. For instance, indirect evidence of eco-field mechanisms in action has been observed in the daily regulation of body mass in European robins (*Erithacus rubecula*) (Thomas 2000). Experiments where food was supplied *ad libitum* to wild birds have demonstrated that birds forage until they reach the same body mass at dusk, regardless of the body mass at dawn. This is a strong indication of a strategy to handle not at random but following precise rules, a vital function like foraging that is in balance with predation and other probable functions. Definitively, the habitat of a species is the summation of the different eco-fields. The ecofield hypothesis allows the entry of more details inside the habitat concept (Franklin et al. 2002). Every species perceives land mosaics differently (Etzenhouser et al. 1998) and should select habitats with the highest score in terms of each eco-field. Some habitats have a higher score for a specific eco-field and lower for others. This fact creates different selective pressure at the population level. Some geographic areas have high scores for a specific eco-field and lower for others; this allows a species to persist but the result is affected by an area-specific environmental pressure. This fact is in line with the theory of evolution and with the struggle for survival. Recently, Pulliam (1988, 1996) has described some sources and sink populations and habitats, posing the question that habitat quality is based not on binary choice 0-1 but on a fuzzy mechanism. The paradigm of the eco-field requires empirical verification but opens a new era of integrated investigation between behavioral, ecological and evolutionary research (Mitchell & Powell 2002).

It emerges from the experimental manipulation of animal movements that in heterogeneous landscapes, behavior assumes importance in the structure of the habitat. For instance, Morales & Ellner (2002), testing random models on *Tribolium confusum*, argued that observed behavior heterogeneity reduces the efficiency of random models to describe the animal movements in an experimental arena. It is also well documented that the physiological state of individuals affects their movements and behavior (Bell 1991).

The paradigm of the eco-field can be utilized to investigate the relationships between plants and their environment. Plants, like animals, are cognitive organisms but differ from animals for lack of an explicit intention and conscious awareness. Plants can be considered as second-order multicellular organisms with a cognition no different from the first-order cells that compose them. The eco-fields in plants are detected by the changing rate of growing roots, branches and leaves, increasing or depressing the chance of survival of seeds, and young and adult plants. As pointed out by Callaway (2002), plants probably detect their neighbors and, consequently, they do not respond only in terms of resource availability. Most of the investigations have focused on avoidance mechanisms at root and shoot level, but others (Gersani et al. 2001) have found in soybeans an increased root growth when shared with conspecific competitors.

The eco-field approach can solve problems linked to the difficulty in connecting the patterns of biodiversity with the landscape characters as warned by Janneret et al. (2003) when using a set of organisms.

In the debate regarding the definition of habitat and the selection of environmental variables that describe the relationships with species and their aggregations (populations, guilds, communities), the eco-field hypothesis reduces the uncertainty intrinsically considered when environmental attributes are coupled with species distribution and abundance (Cushman & McGarigal 2004). In fact, the eco-field hypothesis assumes that a species enters into a semiotic relationship with the surroundings when a living function is active. The "traditional" approach to considering environmental variables chosen according to the perception of the investigator does not allow correlation, by using an explicit model, the life trial and the surroundings. Often, several variables are selected and then condensed using a PCA procedure to extract the principal axes of this statistic. There is no evidence that a species can react contemporarily to so many variables at a time. Often the gradient necessary to perceive a change into the variable behavior requires an unknown time-space scale. We agree with the conclusion made by Cushman & McGarigal (2004) that a decision in terms of habitat preferences is achieved using hierarchical decision mechanisms, but the sensitivity to environmental variables should be restricted to a few cues. The integration of the different decisions requires other mechanisms, from which emerges the individual specific performance. For instance, the role of bird colonies as information centers for other organism has been emphasized by Bayer (1982).

Hunter et al., (1995) have used nest and daytime roost sites of the northern spotted owl (*Strix occidentalis caurina*) to evaluate the "breeding and roosting environmental requirement (Figure 1.19). From the investigation emerges a strict correlation between nonvegetated and herb, mature and old-growth, index of fragmentation and index of heterogeneity, and plot radius at which investigations have been carried out. This figure shows the space of pertinency requested by this species to select both breeding sites and daytime roosts.

Assuming that connection of the individual with the surrounding interacting mechanisms must exist, such mechanisms must use organic codes (*sensu* Barbieri 2005), which are not considered in an ecological investigation. Codes represent the necessary step to connect the inner and outer world

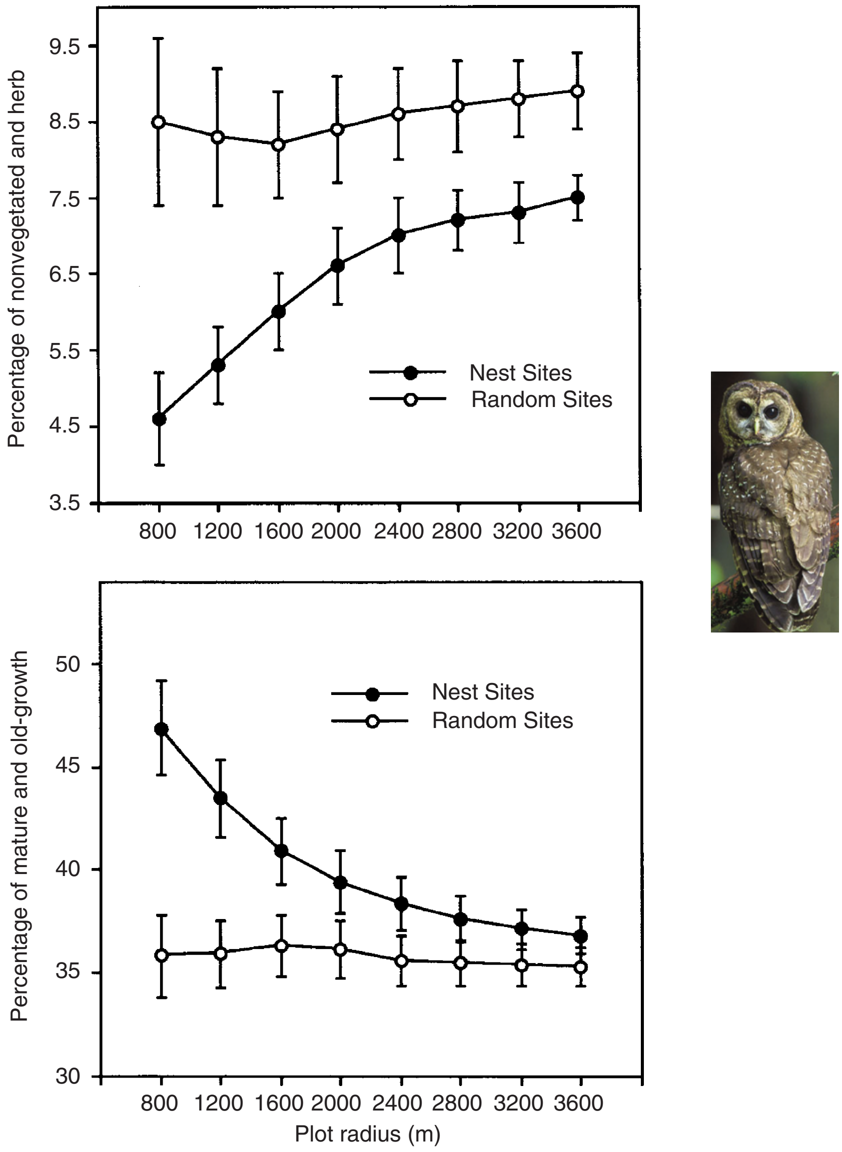


*Figure 1-19.* Presence of nonvegetated and herbs, mature and old-growth, fragmentation and heterogeneity inside circular plots of 800 m each around spotted owl (*Strix occidentalis caurina*) nest sites in northwestern California (from Hunter et al. 1995, with permission).

of organisms. Probably, several codes are contemporarily active but to understand the mechanisms it is necessary to select the eco-field hypothesis via the functions that were working at that specific time.

The eco-field hypothesis appears to be of great utility to efficiently convert the landscape species concept into practice. According to this principle, a species is selected according the requirement of "using large, ecologically diverse areas and often with significant impacts on the structure and function of natural ecosystems" (Redford et al. 2000 quoted by Sanderson et al. 2002).

The eco-field hypothesis can be extremely useful to solve the dilemma of the movement rules of herbivores in heterogeneous landscapes. For instance, Gross et al. (1995), working on the movements of bighorn sheep (*Ovis canadensis*), have assumed that the decision to move from one grazed plant to another follows a nearest-neighbor rule but does not explain the large-scale movements. The eco-field hypothesis can explain the short distance movement betweeen plants as a foraging eco-field characterized by a high density of palatable plants that is elicited by the foraging function. When bighorn sheep move over longer distances, searching for a new foraging area, they require a different eco-field in which the spatial configuration must be based on friction and open paths.

### *1.5.2.11 The soundscape*

Acoustic ecology is a well-developed branch of the ecology that studies the implication of natural and manmade sound on the life of organisms and an area of education, research and practice (but see also Redstrom 1998). The acoustic quality of the environment is important like other factors such as air, water and wildlife, but those are more popular in ecological curricula. Sound pollution is a matter of fact in urban areas, close to airports and roads, and a source of health problems and economic concern. For instance, in Sweden, 25% of the population is exposed to a traffic noise level $L_{Aeq24h}$ >55 dB (OECD 1996). To remedy this, stressful environmental factors, intensive investigation and an efficient methodology are necessary (Skanberg & Ohstrom, 2002; Larking et al. 1996). The proximity of residential settlements to industrial or logistics areas poses the problem of noise assessment, monitoring, design (Truax 1999) and remediation. Auditory scene analysis is central in the curriculum of acoustic ecology and requires both a perceptual semantic approach and physical descriptions (Raimbault et al. 2003). In fact, the same acoustic phenomenon is perceived differently by people according to the context, but a good correspondence has been found between the sound level and the semantic description of the perceived sound.

Landscape ecology has rarely considered the quality of the environment in terms of acoustic cues. However, it is time to insert this argument in the mainstream of landscape ecological research. Of particular importance in acoustic ecology is the relationship not only between man-made noise and animal communication, but also between animals and the landscape mosaic.

Sound can be interpreted as a noise or a song. Sound is produced by pressure on the air by energy. Such perturbation plays a primary role in the life of most animals. Sound propagates in the air according to environmental constraints like sound buffers or reflectant surfaces. Similar to the case for visual landscapes where there exists an acoustic landscape affected by human and also by natural processes. The evaluation of the soundscape could improve our capacity to predict some types of biodiversity or simply the quality of certain ecosystem services. The acoustic landscape is an important component of the living system and sound patterns are strictly connected with the landscape shape and patch composition.

The effect of noise in human environments has long been considered a pollution source but only recently have the effects on wildlife been recognized as an important source of disturbance (Radle 2002). In particular, birds are dispensers of natural music and the chorus of birds in springtime is an amazing, fascinating emergence that can be completely covered by human noise.

Background noise produced by natural processes like falls or wind may reduce the capacity of organisms to understand acoustic signals.

Recent studies have demonstrated that birds like nightingales (*Luscinia megarhynchos*) react to background noise by an increased sound level, which is higher when the acoustic disturbance falls in the spectral region of their own song (Brumm & Todt, 2002) (Figure 1.20). This demonstrates the fact that the nightingale modifies vocal emissions according to the type of background noise in order to maximize song communication. In a successive research, these authors (2004) have found that the reactions of conspecific songs were higher than when animals were tested with a heterospecific song. Birds like tits have been observed to increase loudness in noisy urban areas (Slabbekoorn & Peet 2003; see also Katti & Warren 2004) (Figure 1.21). This effect, called the Lombard effect (from the first biologist that recognized a relationship between environmental noise and acoustic performances), has also been observed in blue-throated hummingbirds according to both naturally and experimental-controlled changes in ambient noise levels (Pytte et al. 2003). Other birds have the capacity to reduce song degradation and react to experimental "near" and "far" songs in a fashion that supports the hypothesis of distance estimation by acoustic cues (Fotheringham et al. 1997).

If birdsong is considered in general as a mechanism linked to territory demarcation, other hypotheses cannot be excluded. In fact, song has been proved to increase the information landscape, attracting other conspecifics as described by Schaub et al. (1999) in migrating Eurasian reed-warblers

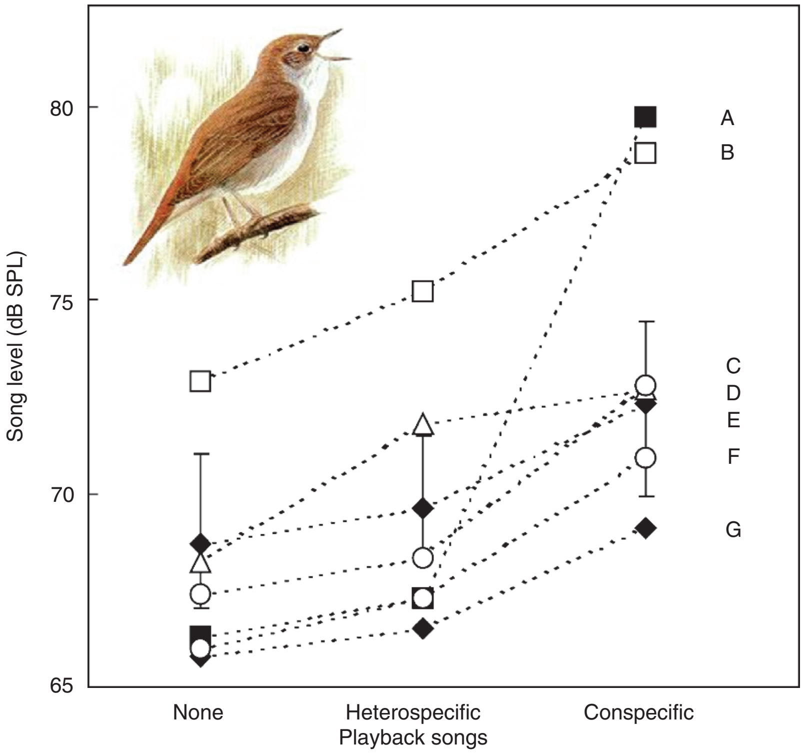


*Figure 1-20.* Average sound pressure level of songs of male of nightingales *Luscinia megarhynchos* (modified from Brumm & Todt 2004, with permission).

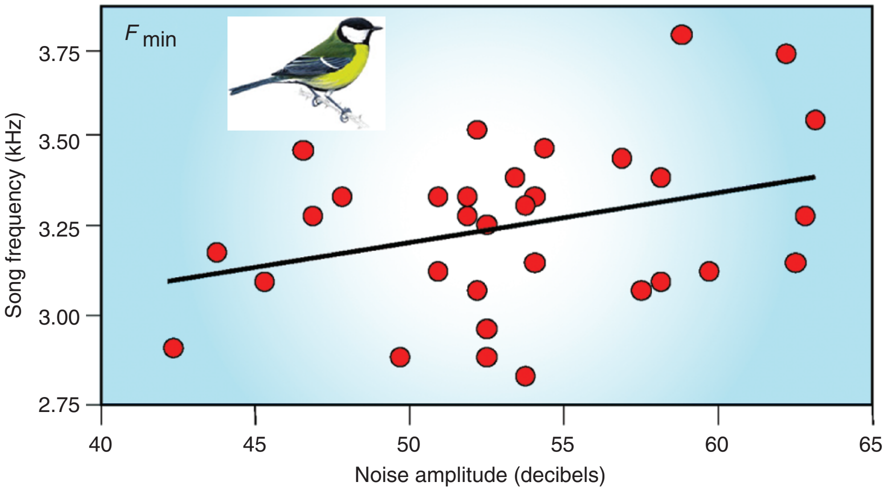


*Figure 1-21.* Correlation between noise amplitude and song frequency of greattits (*Parus major*) singing in urban landscapes (modified from Slabbekoorn & Peet 2003, with permission).

(*Acrocephalus scirpaceus*). Using tape-luring at a stop-over ringing station, these authors have found a significative increase in captures during tape-luring nights.

Birds react to interspecific song, modifying the singing patterns as observed in blue tit (*Parus caeruleus*) by Doutrelant & Lambrechts (2001). This species seems more sensible to the presence of great tit singers (*Parus major*) than to environmental characters (vegetation cover) and intraspecific competition.

Soundscape can be an important component of the foraging eco-field. Montgomerie & Weatherhead (1997) have experimentally demonstrated that American robins (*Turdus migratorius*), in the absence of visual, olfactory and vibrotactile cues, could use auditory cues to locate prey.

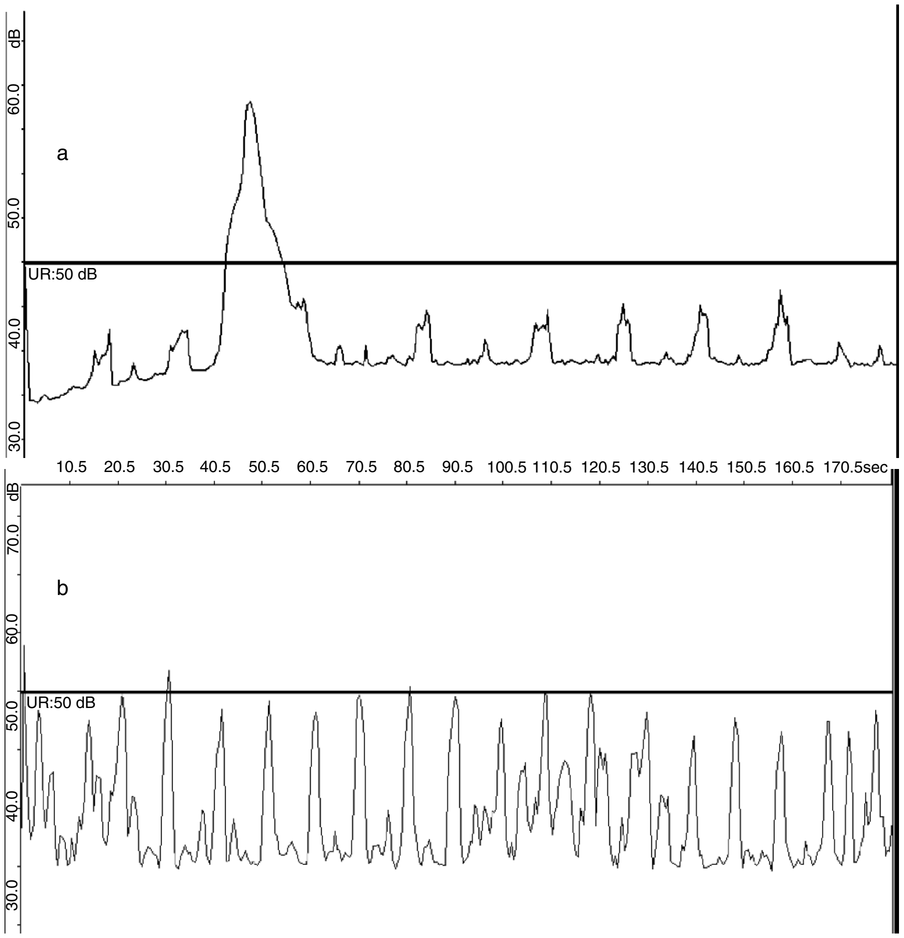


*Figure 1-22.* Examples of sound-scapes recorded using a phonometer (HD 2010, Delta OHM) in different conditions of noise: a. Close to a traffic road b. Far from human disturbance waves are the result of bird song (from Farina, unpublished data).

Long-term soundscape inventories are considered by Maher (2004) as an important protocol to study with scientific methodology the variation in time (day, months, seasons and years) and the quality and quantity of sound in U.S National Parks.

### 1.5.2.12 Animal movements in the landscape

According to the eco-field hypothesis, it is possible to distinguish different typologies of animal movement and to associate a spatial requirement to every typology (Baker 1996). If, on the one hand, the spatial configuration of the land mosaic allows the embodiment of cognitive maps connected to a specific function, on the other hand, it is strongly affected by disturbances introduced by other organisms, like man.

Whittington et al. (2004) have studied the turtuosity and permeability of roads and trails in wolf movement. Wolves demonstrated a major sensitivity to trails in which humans and dogs were common and a source of hostile scent rather than road presence, although when crossing these last, crash occurences were frequent. A olfactory-scape is to be considered under this perspective.

In the study of patch selection in herbivores, there emerges a confounding effect between patch quality and matrix effect, as recently reported by Haynes & Cronin (2004). This effect could be reduced by performing an eco-field approach to the study of animal behavior.

The landscape around us is largely manipulated by our intervention in agriculture, forestry, and development. The emerging mosaic has strong importance not only for species diversity and popolutation abundance but also for several functions that a species performs according to the landscape character. Steffan-Dewenter & Kuhn (2003) have demonstrated how landscape configuration may affect honeybee foraging (Figure 1.23). Locating hives in poorly structured (simple) and in highly structured landscapes and counting dancing activity, these authors observed a higher dance activity in more complex landscapes. The foraging distance of pollen-collecting bees was significantly larger in simple rather than in complex landscapes.

Landscape characters are important elements to create genetic heterogeneity in populations of habitat-tolerant organisms. This is the case studied by Merckx et al. (2003) with two caged populations of *Pararge aegeria* butterflies originating in woody and open landscapes. Woodland populations covered longer distances crossing open-shade boundaries and were more active than agricultural populations. This experiment, considering that both the populations were reared in the same conditions, confirms that the observed differences were dependent on heritable variation, which was fixed into the genetic memory by the environmental constraint.

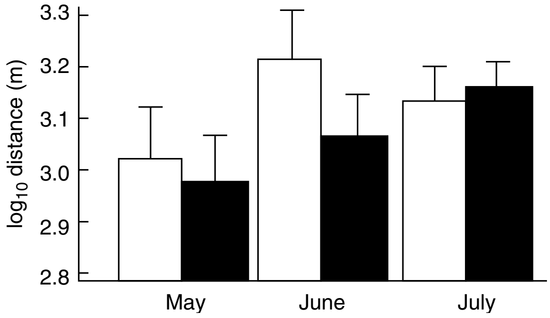


*Figure 1-23.* Number of bee dances per minute in different seasons in simple (open bars) and complex landscapes (filled bars) (from Steffan-Dewenter & Kuhn 2003, with permission).

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## Chapter 2

# THEORIES AND MODELS INCORPORATED IN THE LANDSCAPE ECOLOGY FRAMEWORK

## 2.1 INTRODUCTION

The goal of this chapter is to illustrate the most relevant theories that in some cases are a part of the paradigmatic and theoretical framework of landscape ecology. In the first edition we had included the hierarchy theory, the percolation theory, the metapopulation and the sinks-sources models. Considering the increasing interest of scientists and practitioners in the landscape we have considered other paradigms and theories in order to complete the scenario of a landscape ecology that is moving toward a "science of landscape." Complexity, information, cognition, autopoiesis, and semiotics are the additional paradigms that have to be considered for a better understanding of the landscape as a gestalt entity.

## 2.2 COMPLEXITY

The behavior of the systems has been described in general terms by the pioneering work of Ludwig von Bertalanffy (1969). According to this author, the weakness of past science was represented by the reductionistic approach that has independently investigated the elementary units and ignored the properties emerging from the aggregation of such units. This theory, largely overlooked by a large portion of scientists for its assumed generality, is strictly connected with the complexity theory, although the latter has been considered to be in the positivistic camp while the General System Theory has embraced more interpretivist and critical philosophies (Phelan 1999).

Complexity is one state of the universe but, for many reasons, this condition has been maintained for a long time at the borders of scientific pragmatism. The complexity paradigm can be applied to several disciplines like economics (Arthur 1999), ecology (Limburg et al. 2002) and anthropology (Abel 1998). As argued by Manson (2001), is possible to break complexity research into three main parts: "Algorithmic complexity", "Deterministic complexity" and "Aggregate complexity". Algorithmic complexity takes into account mathematical complexity theory and information theory. The deterministic complexity deals with chaos theory and catastrophe theory. Finally, aggregate complexity considers the holism and synergy resulting from the structural and functional connections between system components.

Complexity is one property of several systems, from the physical to the ecological and social domains. For instance, the complexity theory can be used to investigate how plant communities are structured and self-maintained (Anand & Orloci 1996). Complexity is not a self-explaining process; we need *ad hoc* paradigms to delve inside. As we have already discussed in chapter 1, complexity is born by blending deterministic and stochastic mechanisms. Ignorance of many of such mechanisms is considered in terms of uncertainty by the information theory. Complex systems share common characteristics; are thermodynamically open (far from equilibrium), are composed of a large number of elements; are adaptive; and system components interact each other nonlinearly, are heterogeneous in space and time and have irreversible histories. Complex systems have a critical behavior, implying that a sudden change in state can occur (the percolation threshold (Ziff 1986) as the double jump, or connectivity avalanche, in graph theory (Seely 2000)).

Complex systems have emergent properties, multiscale and hierarchical interactions, self-organization and unexpected behavior (see also Wu & Marceau 2002). The spatial structure of a complex system cannot be represented by classical geometry but by using fractal geometry (Hastings & Sugihara 1993). This seems like the perfect identikit of the landscape and landscape is a ideal arena to test such a theory! In landscape mosaics, most of the processes are "space filling" (seed dispersion, animal migration) and "space clearing" (fires, storms, avalanches, and spatial interactions assume a central role in creating complex landscapes systems) (Green 2000).

### 2.2.1 The emergence of complexity

Different hypotheses can be presented to explain the emergence of complexity, and considering that to investigate complexity, a plethora of mental constructs (Wu & Marceau 2001; Loehle 2004), ranging from neurosciences to genetics, through biological and social sciences, has been created, we have selected three hypotheses with very broad meanings:

- The Uncertainty Hypothesis (UH)
- The Inter-domain Hypothesis (IH)
- The Connection Hypothesis (CH)

#### 2.2.1.1 The Uncertainty Hypothesis (UH)

According to this hypothesis, complexity is a concept connected with the unpredictability of phenomena. Such uncertainty reduces the possibility for a system to couple with another system. For instance, a snow patch on the mountains of the Mediterranean region has no chance to survive in the hot summers of the present day climate, but the shape of the dissolving patch and the rate of melting cannot be predicted on a daily basis. Vegetation has no possibilities to link into a spatially explicit and co-evolutionary matrix, its growing processes inhibited by snow melting.

When a system experiences uncertainty, the information accumulated in a permanent memory cannot be applied and the possibility of ecological surprises is very high. The system moves from linear to non-linear reactions. Uncertainty creates new conditions in which the system develops, recovers or adjusts strategies. To face the uncertainty, a system can only use a narrow range of its redundant functions.

In other words, complexity means uncertainty and this creates new possibilities of stochastic arrangements of patterns and processes. According to this vision we could describe systems like rivers or forests in terms of unpredictability. The point is whether uncertainty is connected with phenomena like species richness or turnover and community coalescence (Tilman et al. 1996).

#### 2.2.1.2 The Inter-domain Hypothesis (IH)

According to this hypothesis, complexity consists in the mechanism by which a domain (Farina et al. 2004) communicates with other domains. To do so, a domain must have a code to be able to convert patterns and processes that have peculiar intra-domain characters. In such a scenario, complexity is represented by the mechanisms acting to assure communication between different systems (Barbieri 2003). Codes and related mechanisms are the expression of such complexity. According to this vision, complexity is the emergence of natural codes that allow a system to communicate with a system located in another spatio-temporal or organizational domain. This hypothesis is very stimulating and has been adopted by many ecologists (Allen & Starr 1982; O'Neill et al. 1986, Allen & Hoekstra 1992). When we study the scalar relationship between systems, we apply the paradigm of complexity as an emergent property of the inter-system coding. Complexity, in this case, is synonym of the language that connects different systems and is represented by coding mechanisms necessary to transfer energy, information (Stonier 1990,1996) and organisms across neighboring systems.

### *2.2.1.3 The Connection Hypothesis (CH)*

The present-day world is becoming more and more connected. This means that energy and information turnover are growing. This has several consequences on the homeostasis of the systems and their survival. It also means a rapid exchange of information among the systems and this can disrupt the insulation required by a system for self-maintaining. We recognize that connections are important to maintain a system, but a system exists only if the self-regulating (autopoietic, *sensu* Maturana & Varela 1980) units persist. If we increase the connections, processes inside the units can degrade their inherent structures due to too much information received and not precisely allocated and the entire system can collapse. More information is intercepted by a system and more sink reactions are expected. The overflow of information reduces the speed of reaction and expands the possibilities of unpredictable results. Using a metaphor, we could compare the processes of the organizing systems to the stationary movement of sea waves. and the emergence of connections to the translatory movement of such waves. Translatory movements disrupt the regularity of the stationary waves. In the same way, the connection between units reduces the stationary, auto-poietic state of such units, thus creating a complex, unstable status.

## 2.3 INFORMATION

When we are dealing with information, we recognize the difficulty of discussing a topic common to many sciences, primarily physics, mathematics, cybernetics, biology and ecology. The difficulty consists in founding a common basis for discussion, either in the content of a general theory of information and especially in ecology, for an initial misunderstanding after the MacArthur & Ranch (1955) attempt at applying Shannon theory to the energy flow of ecosystems (see also Goldstine 1961; Odum 1988; Margalef 1996 and Ulanowicz 2001).

This section has been inspired by a few authors (Stonier 1996; Fleissner & Hofkirchner 1996; Ulanowicz 1997; Ulanowicz & Abarca-Arenas 1997) that have separately considered information as an important component of our universe although attributing different meanings. For Stonier, information is an element of the universe, like matter and energy. For Ulanowicz, it is a status of indeterminacy that transcends the realm of communication theory and for Fleissner & Hofkirchner, it is an emergent character of the system (Figure 2.1).

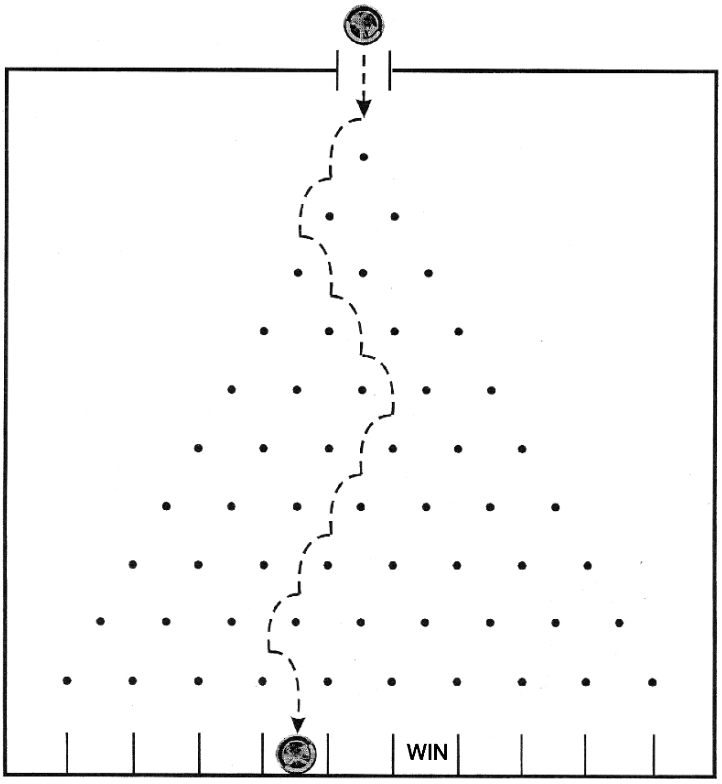

*Figure 2-1.* Game machine to calculate the probability that a coin selects a path at random between the nails, arranged in ten rows, and will win by falling into one of the designated slots. According this probabilistic matrix there are 1024 possible trajectories. The binary logaritmic trasformation produces $\log_2 1024=10$, which is the exact number of events (from Ulanowic 1997, with permission).

Applications of the theories of information to landscape analysis rarely appear in the literature, but as we comment at the end of this section, information theories are of primary importance to developing a science of landscape, because information like energy and matter, is common coinage to many processes. The word information has many meanings in physics, social sciences and biology. For instance, information is associated from media with data. Many scientists consider information to be the way an electromagnetic signal moves from one source to a receptor. The Theory of Information of Shannon (1948) and Shannon & Weaver (1964) should be considered more appropriately as a Theory of Communication, although the famous Shannon entropy equation is actually used world-wide to calculate the diversity of living beings.

### 2.3.1 Information as universal coinage

Stonier (1996) presented a new theory of information assuming that information is a basic property of the universe like energy and matter. Information means organization and, when adequately processed, information produces messages. There exists a direct linear relationship between the amount of heat and energy, and between the amount of mass and quantity of matter; similarly, argued Stonier, there should exist a direct relationship between the amount of organization and the quantity of information.

In this way, we try to trace a mathematical road to symbolically illustrate Stonier's information:

$$-S=k\log Or \tag{1}$$

where S is the entropy, Or is the Order of the system, and k is a constant.

$$I= c(Or) \tag{2}$$

where I is information and c is a constant to be defined

substituting Or of (1) in (2) we can find the relationship between Entropy and Information

$$I=ce^{-S/k} \tag{3}$$

c can be considered the content of information when entropy is equal to 0, and equation (3) can be rewritten

$$I=(I^{\circ})e^{-S/k} \tag{4}$$

Equation (4) states that entropy is the multiplicative inverse of information and not the additive inverse. Shannon and Weaver proposed a direct relationship between information and entropy, and for Brillouin (1956), a negative relationship.

Stonier has also discussed the relationship between energy and information. When you move the dishes on a table you expend energy and this energy is transformed into organization. Organization, contrary to energy, persists until new work is put into the system. Work is a transient phenomena, whilst the product of work that modifies the information status of a system remains. Stonier has calculated that one entropy unit equals approximately 1023 bits/mole and this led to the equation

$$1\ J/^{\circ}K=1023\ \text{bits} \tag{5}$$

Information can be distinguished as structural and kinetic. Structural information pertains to the architecture of the objects, like the shape of an ecotone. Kinetic information pertains to the transient status like across a food chain. Information represents the common coinage that links together a word on a book and the color of bird eggs. Information organizes matter and energy and represents the level of organization of every system.

Order as an indicator of information is the product of energy expended into the system and this causes entropy increase in some other part of the universe.

Information provides a way of quantifying organization and a specific organization is requested in order to maintain living organisms.

Information theory seems a way to measure the fundamental properties of living things.

### 2.3.2 Information as a measure of probability

Ignorance and stocasticity have in common the uncertainty regarding events. And although we can try to reduce uncertainty by using repeated observations under different conditions, some degree of indeterminacy persists. Ulanowicz (1997) introduced information as the result of actions that "refer to the effects of that which imparts order and patterns to a system." This vision is not different from the Stonier vision, by which information refers to order.

It is possible to evaluate the information expressed by an event. Ulanowicz presented a simple example of combinatory calculus. Starting with a probabilistic game based on a vertical matrix of nails that drives in turn a ball (a penny in the example made by Ulanowicz), every nail can be bypassed on the left or the right side by a penny. There are exactly $2^{10}$ or 1,024 trajectories if the nails are arranged in ten rows (see Figure 2.1). The complexity of this system is the result of the combinations of possible encounters and this complexity increases in geometric proportions. In order to know what structure (or number of factors) generate the observed combinations, we can apply the logarithm as an inverse function to the combinations. In this case, $\log_2 1{,}024 = 10$, and 10 are possible factors that have generated the observed frequency. The application of logarithms allows one to calculate the number of events that have generated the observed complexity. Boltzman, followed by Shannon, demonstrated that the application of the logarithm calculus to a frequency or probability generates the number of events that have contributed according to the equation

$$s = -k \log p$$

where p is the probability that a certain configuration will occur, k is a constant of proportionality and s is the potential contribution to the complexity. When an event occurs every time $p=1$ and $\log(1)=0$, this means that such an event has no effect on the complexity of the system.

When a configuration dominates a system, the contribution to the complexity of the system is small; on the other hand, when a configuration is rare, the potential to complicate matters is very high. In order to calculate the contribution of every configuration to the overall complexity, it is necessary to multiply the frequency observed by its relative importance. This can be done adopting the Shannon-Wiener index of diversity

$$H'=-\Sigma pi \log pi$$

This equation is used in ecology as in many other sciences. The strength of this equation is represented by the possibility to be applied to a very broad spectrum of arguments, confirming once more the universality of the information paradigm.

### 2.3.3 Information-processing performance of systems

According to Fleissner & Hofkirchner (1996), systems can be classified according to three levels of information processing along evolutive dynamics: syntactic, semantic and pragmatic aspects, (but see also Cherry 1966). The syntactic refers to a microstate level, semantic to a mesostate level and finally, pragmatic refers to a macrostate level (Figure 2.2).

In parallel, it is possible to distinguish a physical stage, a biotic stage and finally, a cultural stage that are, respectively, coupled with self-structuring, self-reproducing and self-creating (see also Muller 1997).

The physical stage represents the evolution of the physical level that exhibits self-organization by self-structuring in a dissipative thermodynamic way. For instance, a sand dune reflects the wind constraint (direction, intensity) and sand grain.

The biotic stage consists in an autopoietic process that self-maintains and self-reproduces the system, organizing the flow of matter and energy. The system must be able to decodify the signals from the external environment and to establish a meaning for the metabolic necessities. Two relations are involved the sensing and the effectuation.

The cultural stage consists in self-structuring and self-reproducing with an additional property that enables the systems to modify the external conditions of their existence. The structuring of the external environment is a character of this level. A feedback mechanism maintains the connection between the interior aim with the exterior, between the state relation and the output rela-

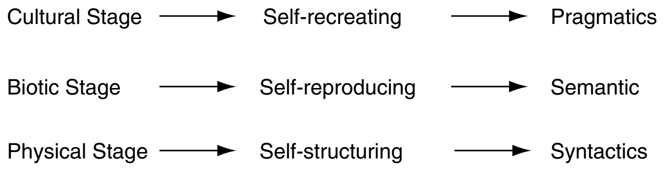

*Figure 2-2.* Level of information processing for an evolutionary system (modified from Fleissner & Hofkirchner 1996, with permission).

tion. This vision is very close to the Umwelt vision of von Uexküll (1940) (see Chapter 1).

Information in a system is created when a surplus of effects exceeds causes.

For Fleissner & Hofkirchner (1996), "information is that part of the process of self-organization that is responsible for generating new features in the system's structure, state, or output". If there are several possibilities for measuring information, we are just at the beginning of developing a theory of the meaning of measurement information (Cropley 1998a,b). We can quantify the amount of signals that move from one source to a receptor but we cannot evaluate the meaning of such information and this reduces our capacity to interpret and use information as an efficient tool to approach complexity.

The information theories appear to be extremely important for landscape investigations, although very few examples are present in the literature (Li 2000). Uncertainty is a very common property in landscape due to the lack of a goal function and aim in the "landscape system." Uncertainty means bifurcation in the dynamics, processes of self-regulation and emergence of order. Patch formation, shape and spatial arrangement are expressions of the information theory either in terms of landscape ontogenesis or communication.

## 2.4 COGNITION AND AUTOPOIESIS

Cognition represents the status of knowledge of interior and exterior of a living organism. Cognition is life, "a continuous complex process rather than an historical logical capability" (Riegler 2002). Every living organism has cognition, which represents the manner of connection with the exterior world (Healy & Braithwaite 2000). Living organisms create a structural coupling with the environment through cognition. Organization and structure, as stressed by Maturana & Varela (1980), are the status of an entity. Organization can persist although the structure is changed. A system is embodied if it is structurally coupled with the environment. This means that a system must maintain environmental feedback in every expression of life, by mutual interactivity. In other words, the system must engage in mutual sequences of perturbations with the surrounding and supporting environment. Unfortunately, human design has difficulty in coping with embodied cognition and transforming a designed system into a cognitive autonomous entity. This has dramatic effects on the landscapes when planning tries to change structure and organization or invents new structures.

The term autopoiesis (from the Greek self and to make, self-producing) has been coined by Maturana & Varela (1980) to explain the characters of living organisms. Apparently, conceptually distant from the landscape paradigm, in reality autopoiesis directly enters several perspectives that have evolved into the arena of landscape ecology. The strictly epistemological approach of these two Chilean scientists is extremely useful for understanding the behavior of individual organisms as well as of systems. Particularly Maturana has hypothesized the possibility to extend the autopoiesis principles to higher-order organisms (Maturana & Varela 1980). This short section is a summary of the work of these two scientists; it is full of conceptual and pragmatic limitations but, nevertheless, we are sure of its usefulness to introduce some basic concepts. Preliminary concepts (Maturana 1999) are necessary for a better understanding of the autopoiesis theory. For instance, "an observer is someone who can make distinctions and specify that which he distinguishes as an entity different from himself." A unity is any entity (material or conceptual) distinct from a background. Interaction emerges when two unities exchange matter, energy and information. The space is the domain of all possible relations and interactions. Explanation is a process that an observer uses towards another observer. Organization refers to the relations between components that produce a unity. Structure defines the space in which a composite system exists. The autopoiesis theory explains how living organisms are self-maintained through interior "programs" that are continuously renovated in order to assure omeostatic conditions. "*Autopoietic machine, as the living organism is defined as a network of processes of production, transformation and destruction of components.....*". On the contrary, an *allopoietic machine* is a system that produces something different from themselves, like a car. The domain of the allopopietic machine is determined by the observer. Autopoietic machines are dominated by omeostatic processes that maintain some of the variables inside a range of values.

Autopoiesis opens the road to the cognitive landscape and is a formidable basis for re-interpreting semiosis, coding sciences and network behavior.

## 2.5 SEMIOTIC, BIO AND ECO-SEMIOTICS

Cognition in landscape science represents an important process. Human landscape is largely perceived by our senses and a mental map of the complexity is the product of cognitive input. Noise, light, color and smell are ingredients of the living world which, in some cases, is extended to the extreme limits of physical behavior (infra and upper tail of the electromagnetic spectrum). The world is full of signals that can be decodified from an interpretant and transformed into signs. This is the conceptual basis of the semiotic, the science of language, according to Saussurre or any action that has three components: the sign, the interpretant and the object. According to Peirce (quoted by Eco 1975) the definition of life coincides with the definition of semiosis. Kull (1998b) defines semiosis "*as a process of translation, which makes a copy of a* *text, suitable to replace the original text such that the original text cannot be used (either spatially, or temporally, or due to the differences in text-carrier or language) for the same functions.*" This creates an endless chain "*every semiosis always requires a previous semiosis.*" Semiosis can be considered as "*the appearance of connections between things which do not have* a priori *anything in common*" (Kull 1998b). In particular, the bio-semiotic (bios=life, semion=sign) is a branch of semiotics that studies communication and signs in living organisms (Kull 1999a). The term Biosemiotic was firstly used by F.S. Rothschild in an article published by the Annales of the New York Academy of Sciences (1962:777) (Kull 1999b), although Uexküll (1909) was the first to discuss the bridge between biology and semiotics, as reported by Sharov (1992). Marginally considered in biology and ecology, biosemiotics can contribute to better understanding of the cognitive processes shaping the landscape. We can distinguish a vertical from a horizontal semiosis. The vertical semiosis represents the way communication crosses the different inner parts of an organism, creating semantic closure. This vision is strongly related to the autopoiesis hypothesis. The horizontal semiosis consists in the transfer of messages from one organism to another.

An interesting evolution of bio-semiotics into eco-semiotics appeared recently. This new branch of semiotics has been defined as the semiotics of relationships between nature and culture (Hoffmeyer 1996, Kull 1998a) but also as the semiotic relationship between organisms and their environment (Noth 1998; Emmeche 2001) (Figure 2.3).

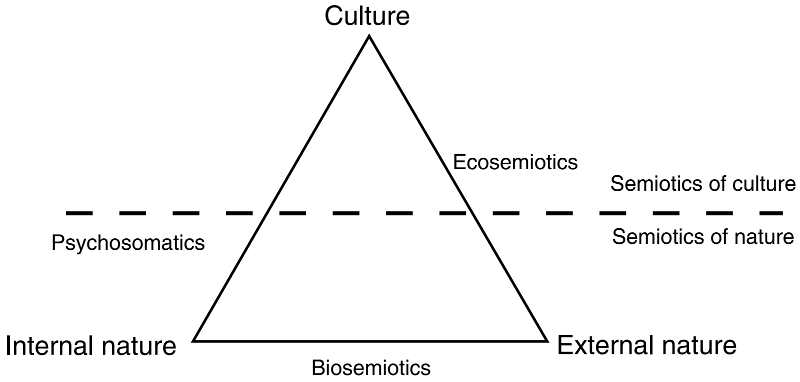

*Figure 2-3*. Representation of the eco-semiotics in relation with the biosemiotics and psychosomatics. Internal nature is represented by living organisms. The external nature of all living and non living organisms outside the organism (from Hoffmeyer 1997, with permission).

Hoffmeyer (1997) argues for enlargement of the ecological niche to a semiotic niche in which a set of signs of visual, acoustic, olfactory, tactile and chemical origin enter into the heredity of a species, assuring the chances of survival (semiotic fitness).

Most bio-semioticians refer to the extraordinary scientific contribution of Jacob von Uexküll in the first half of the previous century. The Umwelt represents the subjective universe created by organisms using a semiotic procedure. The ensemble of the Umwelts that enters into contact creates a new phenomenological dimension that Yuri Lotman (1984) (quoted by Kull 1998b) defined as the "semiosphere". Usually, semiotics and biosemiotics consider animals and humans but recently Krampen (1981, 1992) has enlarged it to plants (see also Kull 2000).

In conclusion, the contribution of bio-semioticians to the interpretation of the living complexity has dramatically increased during the last decennia. Although there is a disparity in approaches and paradigms, it seems that semiotics can improve biological and the ecological knowledge. The dual vision of a world composed by a matrices of invariant systems and by autopoietic organisms that create and invent semiotic matrices (variant systems) is in accordance with the complexity paradigms. The description of a landscape based on ecological processes can be paired to a landscape created by bio-semiotic processes. The landscape can also be considered as a mosaic of ecological and semiotic processes.

The difference between these two mosaics consists primarily in the open character of the first. The energy enters, is dissipated and transformed into information by decodifiers. In the latter, information is not created simply by the input of external energy but by the creation of new relationships between the composite systems (by adaptive evolution). Semiosis is a highly creative system linked with the biochemistry and the evolutionary forces that dominate the ecological landscape.

If we consider the novelties in the mosaic configuration, such novelties substitute the old ones by a temporal process. The new configurations are like unknown systems that can open a dialog with the old ones, like a new language introduced by an immigrant. This means, in ecological terms, a lack of exchange of organisms or processes. When two adjacent systems have no communication, they persist separately and cannot be included in an ecosystem framework; the systems do not evolve into a meta-system and complexity is a process out of order.

## 2.6 THE HIERARCHY THEORY AND THE STRUCTURE OF THE LANDSCAPE

Hierarchy represents a very useful theory in landscape ecology to explore many patterns and processes across different levels of spatio-temporal scales.

Considering complexity as an intrinsic attribute of a landscape, the hierarchy paradigm explains how the different components, localized at a certain scale, are in contact with the other components visible at a different scale of resolution.

The hierarchy theory considers a system as a component of the larger system which, in turn, is composed of subsystems. Moving from one level to another of the system, the characters of the phenomena change.

Landscape classification is one example of a hierarchical framework moving from ecotope across micro-, meso-, macro and megachores. River watersheds are examples of a hierarchical system. A river basin is composed of sub-basins, and each sub-basin is again composed of smaller order basins (Figure 2.4).

Complexity is a fundamental part of the hierarchy concept. The more components that are included in a system, the more complex the system becomes. For this reason, we can consider landscape as a very complex system.

A system exists independently from his components. A system is generally self-organizing, it can thus be considered a cybernetic organization. Landscapes have an organized complexity and in order to understand a system it is necessary to focus on the level of organization. In fact, considering the complexity of a system, it is important to select the best spatio-temporal scale at which the phenomena are related.

The complexity of a system can be decomposed in vertical and horizontal structures.

*Vertical structure:*

Assuming a vertical structure, we expect a behavior to occur at a slow rate. For example, leaves respond very quickly to light intensity, increasing the photosynthesis, but the grow of a tree is represented by the integration of short time events. Not all vertical systems are hierarchical; but in a hierarchical system, it is possible to isolate a layer according to different rates. Each layer of the system communicates with the other layers, filtering messages crossing the "border". High frequency characterizes the lower layers of the system, but higher layers have processes occurring at low frequency (Figure 2.5).

*Horizontal structure:*

The horizontal structure of a hierarchical system is composed of subsystems or holons. Holons may also be considered as an interface between the parts and the rest of universe. Every holon is a part of a higher level holon but can be considered as an ensemble of units itself.

The bounds of holons may be visible and tangible as the border of a forest or intangible as the distribution of a population.

One holon may be composed of other holons that transmit an aggregated output to holons at higher levels. This represents a real filter for energy, material and information crossing the different layers. Hierarchy can also be

*Figure 2-4.* In a complex system, organisms and processes may be structured in a spatial and functional hierarchy. In this case, different-sized mammals are associated with stream order (from Harris 1964, with permission).

defined as a system of communication in which holons with a slow behavior are at the top and represent the context in which lower-level holons move faster.

Scaling a hierarchical system consists in separating processes and for this a forest may be considered a durable environment in which a species lives, or a

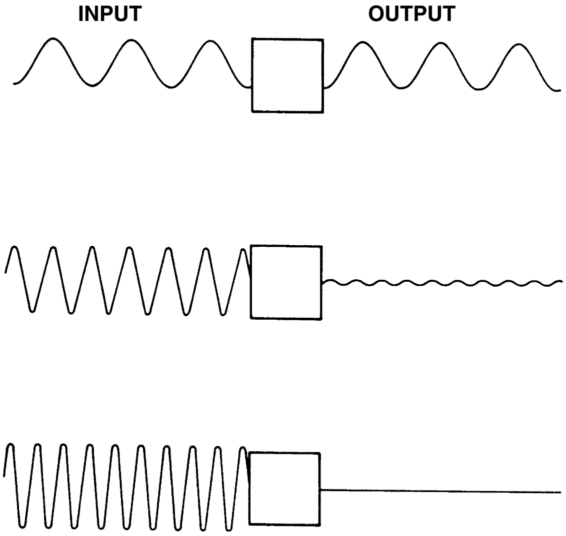

*Figure 2-5.* Changing of input signal when crossing a hypothetical constraint. Low-frequency signal crosses the box maintaining the characters unchanged; increasing the frequency in input produces a smoothing in the output. This behavior is applicable to many natural processes across a hierarchical system (from O'Neill et al. 1986, with permission).

dynamic entity or, finally, simply an echo of a geomorphological process, according to the scale of resolution available. The detection of a level is based on the rate of change of some variables. Generally, where a discontinuity exists, there may be a localized bond of a hierarchical component.

Incorporation is a useful concept when we observe the behavior of a system facing a perturbation or disturbance. This is defined as the process by which the perturbation is adsorbed by a level of the system.

Fire disturbance can be a good example of incorporating the disturbances of a forest. A fire generally destroys part of a forest but not the entire forest, and the forest survives the fire, incorporating the burned patches. In many cases, fires are necessary to assure high diversity of the forest and, in this case, fire is an incorporated disturbance.

Another good example is represented by the grazing of ungulates. Grass cover suffers as a result of this disturbance but the biomass consumption by ungulates is replaced by a new stimulus to the root systems thanks to nitrogen input released by manure deposition.

When the disturbance is very high and/or frequent, the system collapses and its complexity is reduced. This may be the example of the coastal range of Mediterranean basin, in which human-induced fires occur so frequently that the system does not have the capacity to incorporate the “novelty” (see Chapter 6). In this case, the transformation from a forest to woodland and then to a scrubland represents progressive steps toward a simplification of the system. In this way, only some components of the system survive, but if the disturbance is severe, the system is completely replaced by another system.

The study of ecological complexity has for a long time escaped from ecologists but when we select the landscape scale composed of many ecological elements, we cannot avoid considering the hierarchical arrangement of patterns and processes.

Studying an organism or a landscape, we can consider its internal functioning and also its behavior compared with external cues. In this case, we have two levels: higher and lower. This, in synthesis, is a pattern common to many natural organizations.

Allen & Hoekstra (1992) distinguish five interrelated criteria ordering higher and lower levels:

1. Stronger connections within the component of an organism exist but only cross the surface as weak signals (energy, information).
2. Relative frequency represents the number of time in which an organism repeats a behavior. The frequency is determined by an internal clock. A high level system has a longer return time than a small system. We have many examples available. For instance, large carnivores (lions) feed once or twice a day, but shrews (a few grams of biomass) need food every few minutes to compensate for their high metabolic rate.
3. Context represents the environment in which a lower level is contained.
4. Containment. In a nested system, the higher level behaves more slowly than its parts, in which the whole is the context of the parts.
5. Constraint. The constraint may be considered as the limiting factor of a level. This point and the frequency are important criteria to order the levels and allow the system to become predictable.

Recently, Holling (1992) hypothesized that a small set of plant, animal and abiotic processes structure ecosystems across scales in time and space. These processes should have dominant temporal frequencies that control other processes. These frequencies generally differ from each other at least by an order of magnitude. In this way, we can expect the ecosystems have a few frequencies endogenously driven and discontinuously distributed.

The discontinuity of frequencies is coupled with discontinuity’ distribution of spatial structures. Thus, animals living in such a system should have gaps in the distribution of their size, according to the available landscape structure.

Holling tested his hypothesis of body-mass clump distribution in different ecosystems (forest, grassland and marine pelagic) and on different animal groups having different body plans (birds and mammals) and feeding habits (carnivore, omnivore and herbivore). He found at least eight habitat “quanta”, each defined by a distinct texture at a specific range of scale, covering tens of centimeters to hundreds of kilometers in space and from months to millennia in time.

The processes that influence the structure move over limited scale ranges. Behavior and morphological attributes of animals can be used as bioassays of the landscape structure or as predictors of the impact of changes in vegetation patterns on the animal community structure.

## 2.7 THE PERCOLATION THEORY

This theory, formulated to study the behaviour of fluid spreading randomly through a medium (Stauffer 1985), has found an interesting application in landscape ecology, in particular for the preparation of neutral models (Gardner et al. 1987).

In the diffusion process, like the irregular thermal motions of molecules in the liquid, any diffusing particle can move and reach any position in the medium.

The percolation process is quite different. A percolation threshold marks the differences between finite regions in which fluid remains when the percolation threshold pc is < 0.5928 (also called critical probability) (Ziff 1986) or the fluid crosses the lattice connecting every molecule of fluid with the others when p (probability) > to pc (Figure 2.6).

In large lattices, the number and size of clusters is a function of p (probability that a cell is occupied by a target object that can be a vegetation type or an animal distribution). The behavior of the clusters changes rapidly around

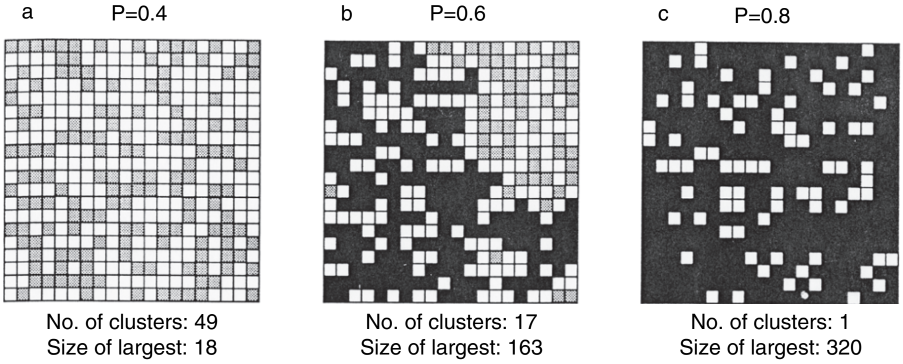

*Figure 2-6.* Example of three random maps (20 x 20 ) with different values of percolation: (a) no percolation p=0.4; (b) percolation p=0.6; (c) percolation p=0.8 (the percolation cluster is indicated in black and the other occupied cells in gray) (from Gardner et al. 1992 with permission).

the critical threshold pc. If we measure the number of edge cells, (i.e., the cells that are adjacent to unoccupied map sites) according to the value of p, it is possible to predict the amount of total edge and of internal edges according to the fraction of the map occupied (p).

The importance of the percolation theory in the study of landscape characters is quite clear when we consider that contagion effects, disturbances, forest fires, and pest outbreaks have their starting points near pc (=0.5928) (Turner 1987). Percolation theory has been employed in the study of landscape boundaries (Gardner et al. 1992).

Considering a matrix composed by m×m cells, the extension of ecotone across a cluster depends on the probability p to occupy cells. Figure 2.6 reports three examples of p at 0.4, 0.6 and 0.8 occupancy. The highest level of clusters is shown by the matrix with p occupancy probability of 0.4. No clusters are percolating. In case b, a cluster is percolating and the number of clusters has been reduced by approximately one half compared with the first example. In Figure 2.6, only one cluster is present with a probability p=0.8. According to this behavior, we can predict the amount of edge (total and inner) in the matrix. Figure 2.7 reports the amount of edges according to the fraction of the map occupied.

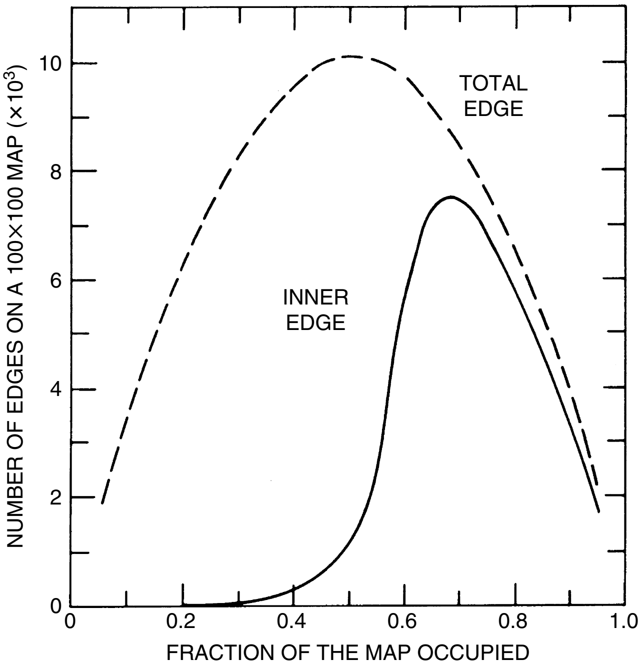

*Figure 2-7*. Number of edges in the fraction of the map occupied (p) (from Gardner et al. 1987, with permission).

The percolation theory finds application in the study of animal movements and use of available resources. When an animal moves in a habitat that has value equal or higher than pc=0.5928, the organism can cross the entire landscape.

Assuming that an organism can find at least 1 resource moving for n units of landscape, the probability of finding 0 resources is (1-P)n, where P is the random distribution of a resource. The probability R to find at least a resource is

$$R= 1-(1-P)n \tag{1}$$

We know from the percolation theory that if R=0.5928, then an organism can move from one part to another of the landscape.

Substituting R in equation (1) and rearranging, we can find the relation between n and P:

$$n=-0.89845/\ln(1-P) \tag{2}$$

Equation 2 allows us to calculate the scale at which an organism interacts with the environment when the resources have a P distribution (Table 2.1).

If the resources are concentrated (P close to pc threshold), the number of landscape units to be explored by an organism to find resources is very low, but by decreasing the distribution of resources, the number of units to be explored have to be increased (Table 2.1).

If resources are two or more the n"=-0.89845/(ln(1-P1)+ln(1-P2)), where P1 and P2 are, respectively, the distribution of the two resources. Evidence of this mechanism is reported by O'Neill et al. (1988). When a dominant organism removes 90% of the resources, the subdominant organism has available just 10%. In this case, to find the amount necessary, an organism has to move around to find other resources. As predicted by equation 2, large-scale sub-dominant organisms are rare when sampled at a small scale.

*Table 2-1.* Number of n landscapes units searched by an organism with a Pi distribution of resources (from O'Neill et al. 1988, with permission).

| *n* | *Pi* |
|---|---|
| 0.1 | 0.592800 |
| 0.4 | 0.201174 |
| 0.9 | 0.095007 |
| 0.16 | 0.054606 |
| 0.25 | 0.035300 |
| 0.100 | 0.009844 |
| 0.400 | 0.002244 |
| 0.900 | 0.000998 |
| 0.1600 | 0.000561 |
| 0.2500 | 0.000359 |

## 2.8 THE METAPOPULATION

### 2.8.1 Introduction

The increase of forest fragmentation as a general trend in natural habitats, has created small and isolated woodlots containing less species than surrounding woodlands. The reduction of species has been attributed to the high rate of extinction (Figure 2.8). When populations are living in a heterogenous environment and can be isolated from each other by hostile or less favorable habitat, and the contacts with each other are assured only by emigration or immigration processes. The risk of local extinction and the probability of recolonization mainly depends on the capacity for maintaining an exchange of individuals. Colonization success depends on many factors, like as the capacity to disperse. These populations are considered more generally as components of a metapopulation. The colonization ability is essential during the turnover process in a metapopulation.

The term metapopulation has been introduced by Levins (1970) to describe a population of populations (Gilpin & Hanski 1991, Hanski & Gilpin 1991). Instead of focusing on a population, Levins considered a set of subpopulations that are actively in contact with each other. Metapopulations are systems in which the rate of extinction and recolonization creates a flux of individuals, which assures genic connectivity among the sub-populations. This is a very frequent condition in disturbed and fragmented habitats. The genetic or demographic connection is the necessary factor for creating a metapopulation; as

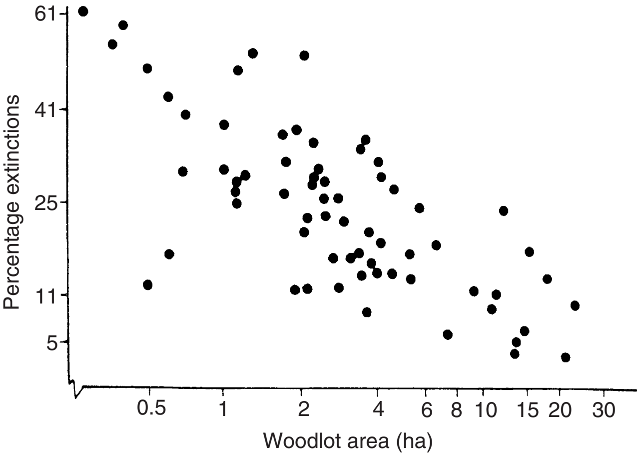

*Figure 2-8*. Effect of fragmentation on percentage of extinction of bird species in mature deciduous and mixed-forests in a farmland mosaic (from Opdam et al. 1994, with permission).

opposed to now we are in presence of separate populations. For this reason, the fortune of this definition and the demographic rules built around this concept have found great success during recent years.

The metapopulation concept is strongly related with the island biogeography (MacArthur & Wilson 1967), considering both colonization and extinction as fundamental processes. In particular, the inclusion of the metapopulation concept in the body of landscape ecology concepts contributes to a strong ecological synthesis.

Despite a relatively common agreement of the concept of metapopulation as a dynamic process of species distribution, many different opinions exist on the mechanisms that operate (Figure 2.9). Most of these belong to the population demography discipline and have only marginal interest for our landscape approach (see also Hill et al. 1996; Peltonen & Hanski 1991), although recently Hanski & Ovaskalnen (2000) have introduced the concept of metapopulation capacity as a measure of the capacity of a land mosaic to support viable metapopulations and defined it as a leading eigenvalue of an appropriate "landscape" matrix (Figure 2.9).

## 2.8.2 Dispersion

Although in the past reproduction and mortality were considered important and exclusive patterns of the population processes, dispersion appears to be a very important factor governing the demographic and spatial structure of

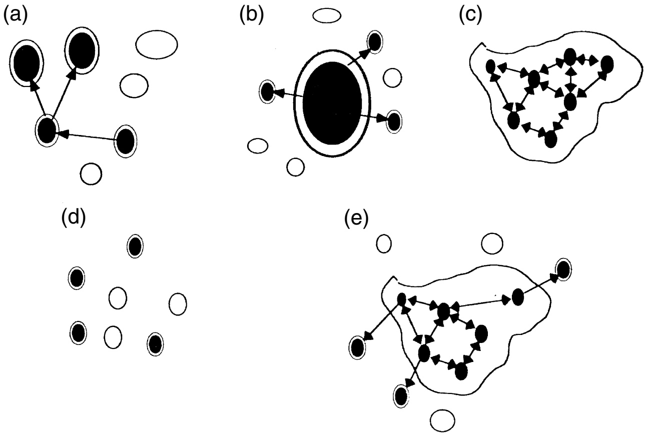

*Figure 2-9.* Different types of metapopulation models. Filled circles = occupied, Unfilled = vacant, Dashed lines represent the boundaries of a population, Arrows indicate migration. (a) = Levins metapopulation; (b) B = Core-satellite metapopulation; (c) = Patchy metapopulation; (d) = Non-equilibrium metapopulation; (e) = A combination of C and B type (from Harrison 1991, with permission).

the metapopulations. Hansson (1991) has recently considered three main factors responsible for dispersion, presenting a review on dispersal mechanisms:

Economic threshold. An individual moves from one patch when the level of resources like food supply moves below critical levels. The dispersion is very frequent in temporary habitats.

Conflicts over resources. Generally, dispersion is a necessary mechanism to escape competition for limited resources like food, breeding sites and water availability. This mechanism may be present in female versus male dominance, young against adults, inferior social categories against dominant ones.

Inbreeding avoidance. This may be a proximate or an ultimate factor. This factor seems density independent. Hansson also considered the timing of dispersal, the genetic differences between individuals, the demographic differences and the spatial extent of dispersal as components of a complicated mechanism that moves individuals and populations in the constellation of metapopulations.

### 2.8.3 Examples of metapopulation structure

*Melitea cinxia* populations studied by Hanski et al. (1994) on the Baltic Aland island shows strong evidence that long-term persistence largely depends on the “genuine extinction-colonization dynamic”. An extensive migration was found that affects the local density. The demographic and dynamic model of this species, in which sub-populations are not really very isolated, seems common for other species of butterflies.

In *Rana lessonae* living in ponds, the rate of extinction depends on deterministic and stochastic components (Gulve 1994). The deterministic extinction is mainly caused by the ponds’ disappearance for drainage or by natural succession. Extinction in permanent ponds depends on population stochastic processes and the low rate of extinction found in permanent ponds (maximum 8.5%) strongly indicates that the correlation between ponds reduces the effects of the local extinction.

### 2.8.4 Metapopulation and conservation biology

The metapopulation model is extremely useful when applied to species conservation in fragmented environments (Figure 2.10). Recently, Opdam et al. (1994) have discussed the landscape ecological approach as the basis for spatial planning. Fragmentation is dangerous when the patches are isolated and the metapopulation model cannot work. This point will be discussed in more detail in Chapter 6.

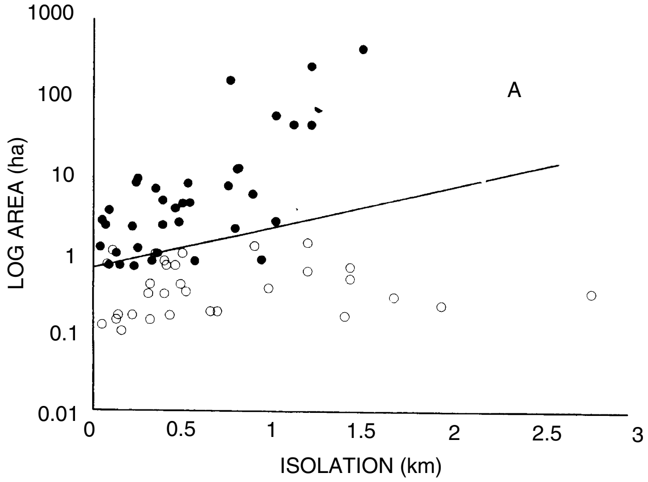

*Figure 2-10.* Effect of area size and island isolation on the presence (black dot) and absence (open circle) of the Shrew *Sorex araneus* on islands in two lakes in Finland (from Peltonen & Hanski 1991, with permission).

## 2.9 THE SOURCE-SINK SYSTEMS

### 2.9.1 Definition

A source is a population in which births exceed deaths and emigration exceeds immigration. At the other end, a sink population has a negative balance between offspring and death and juvenile production does not have the capacity to compensate for the adult mortality (Figure 2.11). In the absence of immigration, a population sink would face extinction. Developed for the first time as a demographic model by Pulliam (1988), the source-sink paradigm finds full reconnaissance, especially after the acceptance of the concept of heterogeneity and land mosaic complexity. Recently, it has been revised (Pulliam 1996) and conceptually enlarged (Dias 1996) (Figure 2.12).

At the same time, we can consider a source patch as a place harboring a source population and a sink patch as the habitat occupied by a sink population.

Until recently, especially in population dynamics, most of the models were considered as homogeneous for every "target" habitat, without taking into account the spatial dimension of the habitats. In this way, every individual experienced the same environmental conditions. But in reality, various habitats inhabited by a species are not homogeneous in terms of resource availability and, for this reason, are perceived as heterogeneous by both individuals and

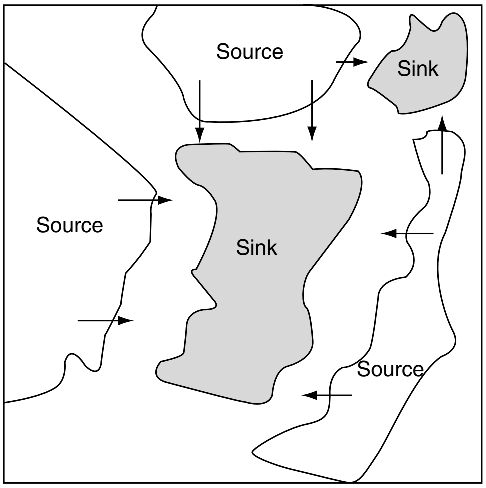

*Figure 2-11.* A representation of a source–sink model. Arrows indicate the migratory flux from source to sink areas.

sub-populations. This paradigm is extremely useful in landscape ecology to explain the different distribution of individuals across the mosaic. It is also strictly linked to the metapopulation concept, having as common basis the different conditions of the occupied patches and the interchange of individuals to maintain the system.

The quality of a patch is largely controlled by the size of the patch. In larger patches, pro capite production is larger and then the source effect more

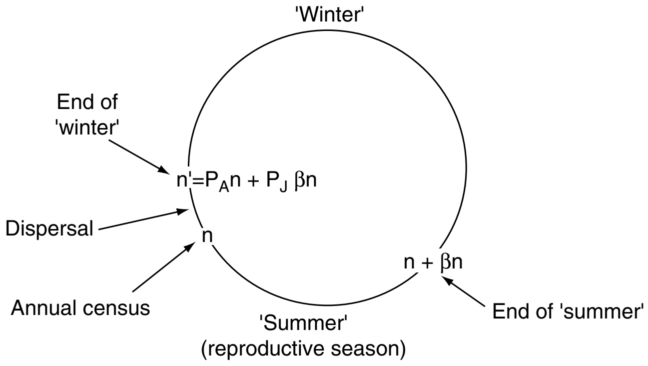

*Figure 2-12.* Demographic model in which at the end of the summer the population composed of n individuals has in total at the end of the reproductive season n+ß individuals where ß is the juveniles alive at the end of the breeding season. At the end of the winter, the survival population n' is composed of adult survival probability $P_A$ and juvenile survival probability $P_j\text{ß}_n$ (from Pulliam 1988, with permission).

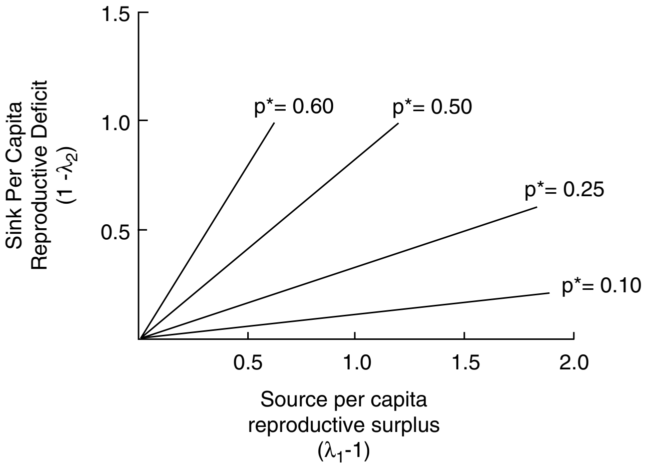

*Figure 2-13.* Graphical representation of population at the equilibrium in source patches (p) as a function of source patch size and sink deficit (from Pulliam 1988, with permission).

evident. The reduction of source patches by fragmentation may represent a serious effect for the survival of a population (Figure 2.13).

Using this model it is possible to intepret some patterns observed in populations of wood mouse *(Apodemus sylvaticus).* This species has been found by Ouin et al. (2000) to fluctuate along the seasons with a early spring – late summer dilution from edges to croplands. This could have strong implications in pest management using a demographic model coupled with a spatial (mosaic) model.

## 2.9.2 Implications of the source-sink model

The attribution of a source or sink character to a patch or habitat is often not easy to determine. For instance, a stochastic event particularly favorable to a species may occur in an unfavorable habitat for a species and creates the wrong conviction that one habitat is of source type. For this reason, particular attention should be paid before deciding the type of habitat. For this, long-term studies are particularly recommended.

## 2.9.3 Pseudo-sinks

Watkinson & Sutherlands (1995) coined the term pseudo-sink to illustrate the situation in which there are two habitats, of which one is more favorable and another less favorable but with good carrying capacities. The poorer habitat is overpopulated by the fact that immigration exceeds the rate of birth/death. The difference between a true sink and a pseudo sink is that if the sink is true, then the population goes extinct if the immigration rate declines, but in case of a pseudo sink, the population will decrease if the immigration is not active but remains although some decline is expected.

### 2.9.4 Traps

In some cases, habitats appear extremely favorable to species although they have no capacities to assure enough conditions for a full successful reproductive cycle. In other words, a trap is a sink that looks like a source (Pulliam 1996). Habitats are common in man-made landscapes in which, for example, food availability attracts a great number of individuals but the human disturbance regime linked to the agricultural practices reduces the reproductive success and, consequently, determines a demographic decline of a species. A habitat is, consequently, extremely harmful for some species. In the case reported by Pulliam (1996) of grasshopper sparrows in the southeastern United States that are attracted by hayfields in early spring but these cultivations are mowed in late spring or early summer before the sparrows have completed their breeding cycle.

### 2.9.5 Source-sink in time or multiple source-sink model

The source-sink paradigm can find interesting applications in landscape ecology even when we consider migratory birds that completely change the living habitat quality. Most trans-Saharan migratory birds have different breeding, wintering and migratory habitats. In this case, apparently, the source-sink model appears of difficult application.

In reality, we could extend the source-sink model to these intricate situations when we can distinguish characters of source or sink in each separate seasonal habitat. One example may be presented when we are dealing with birds wintering in the Mediterranean region. In this case, it could be possible to use this paradigm to define wintering source habitats the habitats in which the survival rate and the emigration in spring is reasonable high. On the contrary, a sink wintering habitat may be represented by a habitat producing a progressive starvation in the animals and consequently a very low success to overwinter.

Although difficult to measure, these conditions are very common in the Mediterranean regions.

### 2.9.6 Stable maladaptation

A particular condition of maladaptation interpretable with the source-sink model has been presented by Blondel et al. (1992) studying the reproductive success of Blue tit (*Parus caeruleus*) breeding in the deciduous (*Quercus pubescens*) and evergreen (*Quercus ilex*) oak forests of southern France (Figure 2.14). The populations breeding in deciduous oaks are well synchronized with the food availability. In evergreen forests, the laying date is the same but it is not synchronized with the food availability that occurs three weeks later. In this case, the reproductive rate is lower. This phenomenon is explained by authors as a maladaptation of the birds that breed in evergreen forests but they immigrated from the deciduous forest. In Corsica, where the evergreen forest is predominant and the blue tit populations are genetically separated by the mainland populations, a synchronization is observed.

During the recent evolution of the forest cover in Europe, an inversion of the source-sink system could have happened in Corsica. In such a case, the

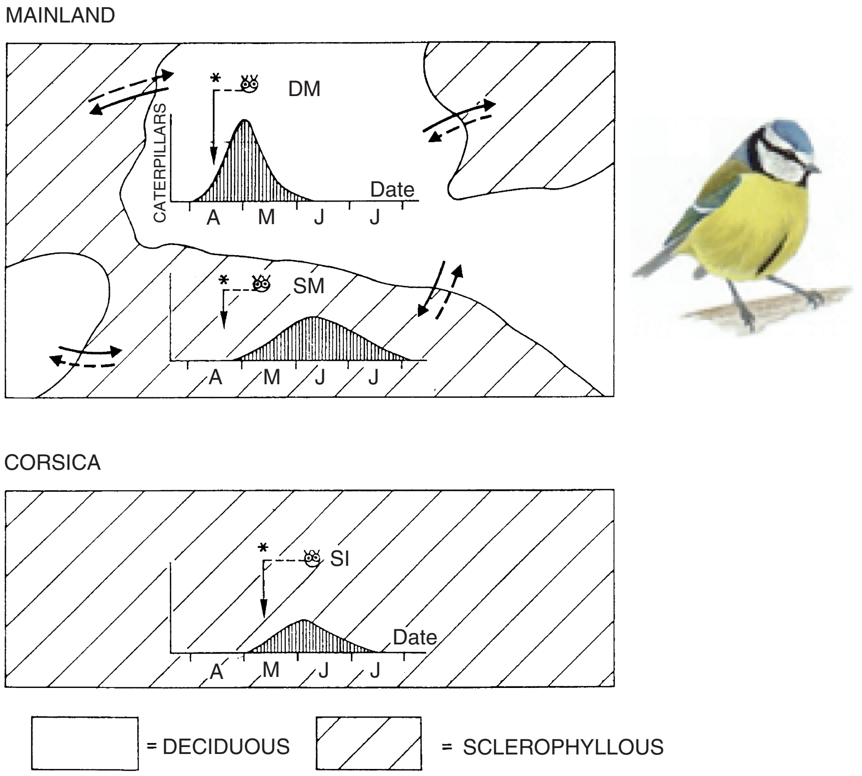

*Figure 2-14*. Example of source-sink system of bluetit (*Parus caeruleus*) in France and in Corsica. In mainland broadleaves, the laying time is synchronized with the food availability, but not in evergreen forests. In Corsica this species, genetically isolated by the mainland population, has a laying deposition date synchronized to evergreen forests (from Blondel et al. 1992, with permission).

change of deciduous oak cover into evergreen cover has restricted the availability of deciduous oak forest and determined an evolutionary adaptation of the blue tit to this new habitat. In other terms, when a sink habitat that generally should not be too much larger than a source habitat becomes predominant, it can create some evolutionary adaptation of species.

### 2.9.7 Source-sink dynamic and conservation issues

Donovan et al. (1995a,b) have prepared a model to verify the effect of fragmentation on a source-sink system of neotropical migrant birds. According to this model, which takes account of the metapopulation dynamic and the quality of the habitat patches, the fragmentation of breeding habitats and common patterns in the boreal regions has a more significant effect in small habitat patches then in larger, core habitats.

In sink habitats, the decline may be higher in small patches and be independent to the source habitat.

This assumption has found evidence and appears useful for managing endangered species. The fragmentation and the strong dynamic of source-sink represents a cost for the populations determining a decline.

The source-sink model has been utilized as a general framework to couple demography and spatial patterns of a forest landscape by With & King (2001) through a spatially explicit model (neutral landscape) in order to provide a realistic procedure devoted to conservation of neotropical forest-interior migratory birds. This type of model provides scenarios useful to manage forest use for timber industries and agricultural development. The effects of landscape structure is highly species-specific and can produce a frustration in land managers that would require a single comprehensive strategy. The species particularly sensitive to forest modification are those with large minimum areas or are highly area sensitivity and perceive edges as a hostile part of their habitat.

The source-sink dynamic requires to be interpreted over a longer period although the sink dynamic may contribute to the overall population size and to assuring longevity. Sink can contribute to gene exchange when the immigration/emigration rate is significant among subpopulations.

### 2.9.8 Concluding remarks

It seems more and more clear that the distribution of individuals often does not fit the availability of the habitat. In this last case, the sink habitat will face the extinction of a population without a continuous flux of immigrants. As pointed out by Pulliam (1996), suitable habitat is often unoccupied, density is not always an indicator of habitat quality, organisms often occur in unsuitable habitats and, in some cases, for some populations, most of the individuals occur in sink habitats. This idea is confirmed in part by island biogeography and in part by the metapopulation paradigm. The source-sink model, on the other hand, also justifies the presence of species in unsuitable habitats. Finally, these two sets of theories explain most of the demographic dynamics of species.

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# Chapter 3

# SCALING PATTERNS AND PROCESSES ACROSS LANDSCAPES

## 3.1 INTRODUCTION

In cartography, scale represents the level of reduction of the real dimensions of the earth and may be absolute or relative. In ecology, the scale is a fundamental concept. In fact, organisms intermingle with the environment using an inherent perception of the surroundings (Powell 1989; Steele 1989). Most of the ecological phenomena show a scale-dependence of measurement and recently, Horne & Scheneider (1995) have reviewed the role of spatial variance in ecology. Although the scaling concept has been used for a long time in ecological research, a special emphasis has been devoted by the plant ecologists (Cain 1943; Cain & Castro 1959; Greig-Smith 1964; Mueller-Dombois & Ellemberg 1974). And, more recently, the concept of spatio-temporal scale has been used as a discriminatory element of complicated processes as the extinction and the recolonization for the formulation of island biographical models (MacArthur & Wilson 1967) and the phenological dynamics of organisms that flow in the atmosphere like viruses, bacteria, pollen, spores, weed seeds, aphids, butterflies and moths and birds (Gage et al. 1999).

Most of the ecologists consider the scale an inherent property of the organism (Wiens et al. 1986; Morris 1987; Dayton & Tegner 1984; Carlile et al. 1989; Maguire 1985; Bock 1987); although some others consider the scale a means to size a phenomenon without explicit influence on patterns and processes (Allen & Starr 1982; Maurer 1985). In our opinion both the assumptions can be accepted according to the context of the investigations (see later in this chapter) and we can adopt the principle that the scale most efficient to investigate a target process is the scale that allows one to collect the maximum information. In fact, moving across the ecological processes, abiotic and biotic interactions have families of scales in which they exhibit emerging properties.

Often, observable patterns are determined by the collective behavior of many small processes moving at different scales; in other conditions the patterns are induced by processes acting at large scales. For instance, to study the flux of nutrients of kelp forests it is not enough to study processes at the local scale. These communities are affected by processes that have scales of hundreds of km. In fact, the type and movements of the sea currents occurs on a broad scale (Dayton & Tegner 1984).

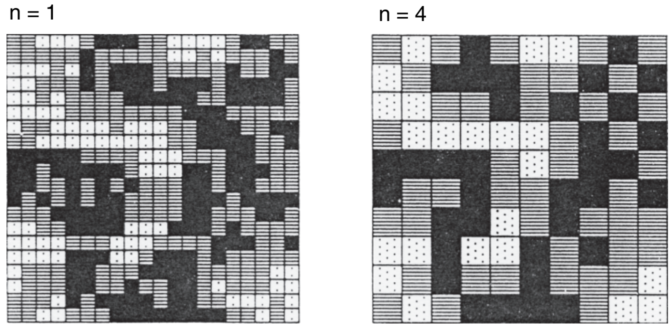
## 3.2 SOME DEFINITIONS

The word scale is employed with several meanings in many disciplines. In ecology, particularly landscape ecology, scale refers to the spatial or temporal dimensions at which an organism or a pattern or process are recognizable. See Table. 3.1 and Figure. 3.1 for more details on terminology and definition (Turner et al. 1989). Changing scale in the analysis of a land mosaic means

*Table 3-1.* Some scale-related terminologies and concepts (Turner et al. 1989, with permission).

| *Term* | *Definition* |
|---|---|
| Scale | The spatial or temporal dimension of an object or process, characterized by both grain and extent |
| Level of organization | The place within a biotic hierarchy (e.g., organism, deme, population) |
| Cartographic scale | The degree of spatial reduction, indicating the length used to represent a larger unit of measure; ratio of distance on a map to distance on the earth surface represented by the map, usually expressed in terms such as 1:10,000 |
| Resolution | Precision of measurement: grain size, if spatial |
| Grain | The finest level of spatial resolution possible with a given data set; (e.g., pixel size for data in raster format) |
| Extent | The size of the study area or the duration of time under consideration |
| Extrapolate | To infer from known values; to estimate a value from conditions of the argument not used in the process of estimation; to transfer information (a) from one scale to another (either grain size or extent), or (b) from one system (or data set) to another system at the same scale |
| Critical Threshold | The point at which there is an abrupt change in a quality, property phenomenon. |
| Absolute scale | The actual distance, direction, shape and geometry |
| Relative scale | A transformation of absolute scale to a scale that describes the relative distance, direction, or geometry based on some functional relationship (e.g., the relative distance between two locations based on the effort required by an organism to move between them) |

(a) Increasing grain size



(b) Increasing extent

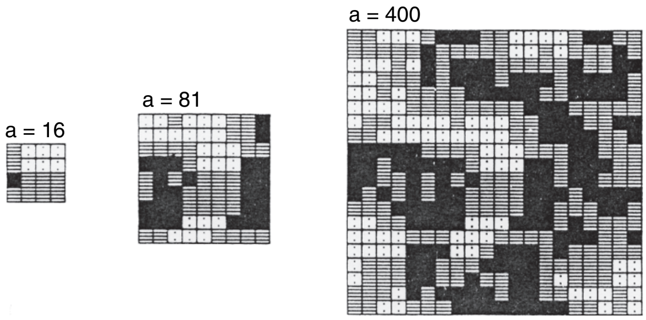


*Figure 3-1.* Two components of spatial scale: grain size and extent. (a) grain size means the minimum dimension of elementary components (cell, pixel). In the example the grain has been enlarged from 1 to 4. (b) extent represents the area considered. The increasing rate of the example is from 16 to 400 cells or pixels (from Turner et al. 1989, with permission).

changing the resolution of cells or increasing the area of survey. A scale may be defined as the period of time or space over which signals are integrated or smoothed for meaning (Allen & Starr 1982).

The use of trivial attributes to describe organisms and their behaviour is often related to human perception. Size, reproductive time, longevity and rates of movements are intrinsically scaled factors. Extrinsic factors are the physical environment and human perception.

## 3.3 MOVING ACROSS SCALES

The comprehension of processes that produce patterns is the essence of science and many global and regional changes of biological diversity, the changes in pollutants, greenhouse effects perceived at a large scale, have origins at the fine scale. Human influence is increasing, affecting patterns and processes at many different scales. Alteration and habitat losses are increasingly frequent and this, for instance, has tremendously depressing effects on biodiversity. To study the environmental problems of our planet, it is necessary to create an interface between many factors that have different intrinsic scales. In conservation biology, to optimize the efforts when resources are restricted, selecting an operative scale appears a priority (Gehring & Swihart 2003) (see Figure 3.2). As argued by Rouget (2003), broad-scale conservation planning is suitable for homogeneous and intact landscapes, but when landscapes are fragmented and heterogeneous, the fine-scale approach is required.

Knopf & Samson (1994) have discussed the use of a multiscalar approach to preserve riparian biota. They recommend to de-emphasize the practices promoting alpha diversity (small-scale approach) and emphasize the scale that allows to consider the beta diversity and long-term processes.

The same conclusion are posed by Sandin & Johnson (2004) after an analysis of the factors structuring benthic macroinvertebrate assemblages in Swedish streams. A multiscale approach is required to understanding the factors that limit populations for wide-ranging species like marbled murrelet (*Brachyramphus marmoratus*), a threatened seabird that forages on the ocean and locates nests inland in large trees, as recently discussed by Meyer et al. (2002). Kunin (1998), working on a different scaling resolution, has described a method to estimate species abundance by extrapolating the scale-area curve using presence-absence maps at varying spatial resolutions.

To accept movement across scales, we have to recognize the hierarchical organization of the ecological systems. Moving top-down means to move toward an increase of detail. On the contrary, the bottom-up movement starts from the individual across the communities, the ecosystems and the landscape. Moving across scales means to accept some levels of bias mainly due to the heterogeneity that influences the processes in a nonlinear way.

Often, human biases are included in the research and interpretation of the results. Recent advances in remote sensing and geographic information systems have offered new opportunities to investigate at scales larger than in the past. And, contemporarily, the research on processes and patterns occurring in the microcosm has reconfirmed the importance of small scales. The expansion of spatial scale has found a consequent enlargement of temporal scale, which by tracking back processes has allowed us to understand the environmental conditions of the past (Delcourt & Delcourt 1988). The availability of data across scales has opened new possibilities to integrate patterns and processes, as recently stressed by Lubchenco et al. (1991).

There are many scales of interest; at each scale some processes are visible because of their pre-eminent characters.

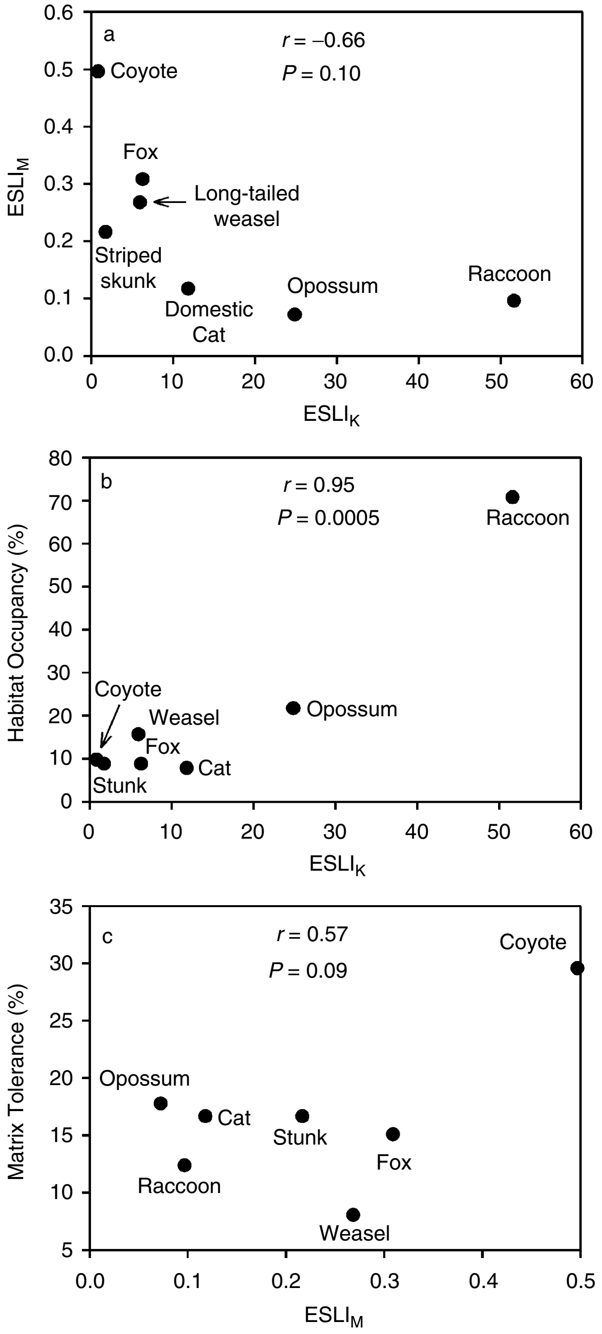


*Figure 3-2.* Ecologically Scaled Landscape Indices (ESLI) of mammalian mesopredators living in an agricultural landscape of west-central Indiana (USA). (a) Ecologically Scaled Landscape Context (ESLI*m*) for vagility versus abundance (ESLI*k*). (b) Abundance (ESLI*k*) and % of habitat occupancy (number of suitable sites visited by species). (c) Relation between WSLI*m* and % of rural matrix (number of scent stations visited in agricultural matrix (from Gehring & Swihart 2003, with permission).

Generally, phenomena are studied using a deliberate scale but often the scale is chosen according to perceptual capabilities or by technological or logistical constraints (Magnuson 1990; Swanson & Sparks 1990; Wiens 1992; Walker et al. 1993).

We define the observation scale as the scale that we can utilize to measure a process, and the process scale or inherent scale is the scale exhibited by the natural phenomena and is independent of our control.

For instance, Chust et al. (2003) have investigated the scale at which the landscape heterogeneity is correlated with the assemblages of Collembola. These authors have found that the heterogeneity appeared at the fourth contrast level (123 ha) at which a remote sensing image has been scanned is negatively correlated with the number of endemic species.

All organisms are conditioned by the intrinsic scale of resolution and generally have the capacities to change this scale according to different situations. For instance, adult animals can have more capacities to explore allocated resources than juveniles because they utilize a broader range of behavior. And dispersal and dormancy are two strategies to change the scale of perception.

To know what information is preserved and what is lost as one moves from one scale to another appears of great interest. Moving across a scale, we can resolve the information from fine scale to a broad scale, in this case we lose details or heterogeneity, gaining in predictability.

Scaling capacities of the organisms allow them to maintain spatial and temporal patterns with consequences on dynamic of populations and ecosystems. Every species experiences the environment on a species-specific range of scales, responding individualistically to the environmental variability.

For instance, Homoptera assemblages have been found to respond to a scale varying between 0.36–2.25 ha, while Dipteran groups were sensitive to landscape metrics at a scale of 316–404 ha for phytophagus, 250–272 for predators and parasites, 1056 ha for saprophagous (Chust et al. 2004).

The local unpredictability and variability allows the species to reduce the competition more than in a constant environment.

Although locally the individual has deterministic replies to environmental constraint, at the population level one may enter stochastic variables into play and the observed patterns receive an irrelevant contribution from the fine-scale behavior. The choice of the sample size and the resolution of quantitative analysis are two sides of the same coin.

## 3.4 SCALING THE LANDSCAPE

In this chapter, we lay emphasis on the importance of scale for studying patterns and processes and the necessity to track phenomena across scales taking into account that in landscape ecology, the hierarchy theory is very popular and largely accepted (Meentmeyer & Box 1987; O'Neill et al. 1989; O'Neill et al. 1991).

Scaling the physical processes like runoff, the spatial distribution of plants and the behavior of animals is an attitude that considers the ecosphere as a hierarchical system in which patterns and processes moving from one layer to another modify their properties.

The scale in landscape ecology, more than in any other field of ecological research, seems a central point around which most of the investigations have to work and presenting the capacity to unify population biology and ecosystem science (Levin 1992; Lawrence & Ripple 2000; Oline & Grant 2002; Verburg & Veldkamp 2004; Wu 2004), working for a real sustainable land use (Steinhardt & Volk 2002).

Most landscape ecological research is posed from a scale of a few meters up to thousands of kilometers, across which most of the ecological processes are completed. The same appears for the temporal scale often considered from the seasonal resolution as in the study of dynamic of metapopulations to the millennia of the biome modification.

A system is functioning across a variety of scales and, when observed at one resolution, we perceive some characters filtering out most of the noise due to the close levels (sub and upper levels) of the entire system's organization.

Different methods of spatial statistics can be successful in studying the variation of processes according to the scale; for instance, fractals, semivariograms, correlograms and spectral analysis.

Patchiness and variability are exhibited by every population across a broad range of scales and such a system is strategic for maintaining ephemeral or competitively inferior species which depend upon the local modification of resource availability and inter-specific competition.

The recent use of remote sensing technologies enables us to investigate local processes across a broad range of scales with the possibility to find the best resolution (Hall et al. 2004). The reclassification of fine-scale imagery by the combination of grain size has been utilized by Turner et al. (2000) to evaluate the best spatial resolution to estimate carbon flux. These authors have calculated a spatial resolution of ≤250 m to capture the heterogeneity expressed by human-dominated disturbance regime.

## 3.5 CHANGE OF PERCEPTION SCALE

If the scale is considered as an inherent character of the species, we could believe that every species perceives and reacts to the neighboring environment at the same scaling metric. But the capacity to change the scale of observation is not typical only of the human mind but many species have the capacity to change their environment perception, for instance, by dormancy and by dispersion. Often the scale issue is more complicated than expected. In fact, most of the species have the capacity to change the scale according to the seasons or internal rhythms. The coarse or fine perception of the environment can change with the season. Some species of birds (f.i. robin (*Erithacus rubecula*)) recognize a site as coarse-grained during the breeding season and fine grained outside the reproductive period. During the breeding season, the robin selects *woodlands*, completely avoiding shrubby and open areas. In this case, it behaves coarsly, the selection is based on wooded/open habitats but outside this period it selects many different (woody + shrubby + open) habitats, then moving as fine grained perceptions of the environment (Farina 1996b).

Changing the scale in the study of animal distribution allows us to understand the proximate factor responsible for abundance. As reported in Figure 3.3, the distribution of robins across two spatial scales allows us to understand how a species shares different habitats, subregions and regions. In the case represented in this figure, the local scale indicates how pairs are distributed in the habitat. At the local scale, the distribution of breeding birds indicates the

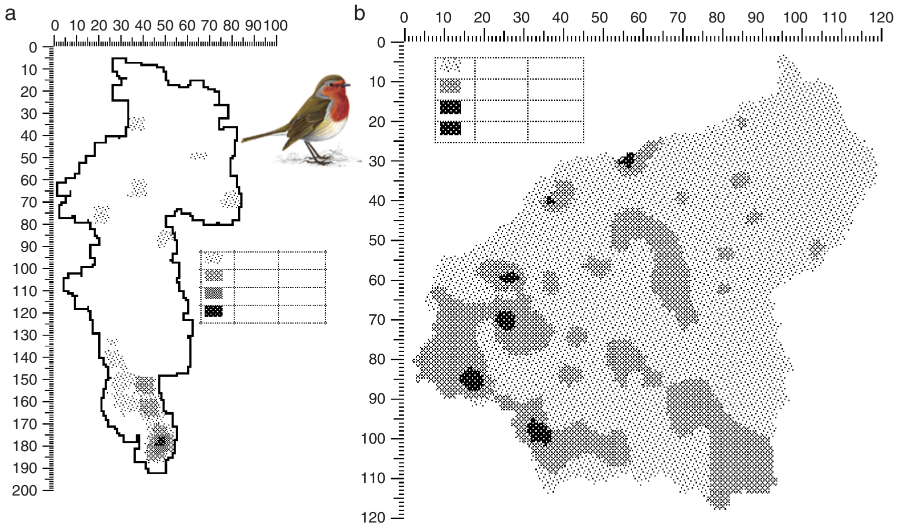


*Figure 3-3.* Distribution of robin (*Erithacus rubecula*) during the breeding season across two different geographical scales: (a) local scale (Logarghena prairies), grain size 20x20 m, extension 2x4 Km (Farina 1998); (b) catchment scale (Aulella river), grain size 200x200 m, extension 24x24 Km (Farina 1997).

variability in habitat suitability across a relatively restricted range of habitat availability. At catchment scale, the effect of slope orientation and the different climatic regime are important factors affecting the distribution of this species. Crossing different spatial scales allows us to investigate nesting selection, habitat selection and regional selection.

## 3.6 THE MULTISCALE OPTION

Many animals, like butterflies, interact with the environment using different scales (Debinski et al. 2001). In *Apodemus sylvaticus* (Muridi, Mammipheres) and *A. flavicollis* (Muridi, Mammipheres), the environmental choice of the habitat is linked by two mechanisms: at the microscale the food availability seems to be the most important factor, but at macroscale the % of rural fields is the discriminating component (Angelstam et al . 1987).

Bald eagles (*Haliaeetus leucocephalus*) are large predators that require heterogeneous landscapes to perform their vital functions. Every function like perching, foraging, freedom from human disturbance requires a specific scaled choice. The environmental analysis to evaluate the suitability of a river for this species, argued Thompson & McGarigal (2002), must be performed at multiple scales of resolution in order to be efficient. Direct evidence suggests that eagles select perching sites not on the stand character but on an individual tree basis. Eagles respond to human activity at multiple scales. At a finer scale, these raptors avoid potential disturbance but on a coarser scale, they select areas with moderate disturbance but where food availability is relevant. On the other hand, eagles avoid undisturbed areas when food is not available.

Carlile et al. (1989) argued that the patterns of vegetation depend on the overlap of factors such as soil composition, nutrients, humidity, topography, etc. These hedaphic factors have a strong effect on vegetation. For this reason, neighboring plots should have a lower variance than the more distant plots, varying the frequency of the sampling along transects and the distance between transects.

For instance, Carlile et al. (1989) have found that sample variance increases as functions of transect segment length and intersegment length and correlation decreases as functions of intersegment length and transect segment length. For this, *Agropyron spicatum* is correlated across the overlap on a scale of 400 to 700 m, and a segment length of 64–128 m is an appropriate scale to measure the cover of this plant (Figure 3.4).

Krill and phytoplankton represent an example of multiscale processes. At a large scale are the sea currents that determine the location of these organisms, but it is at a fine scale that the diving behavior of the krill affects the distribution and abundance of the phytoplancton.

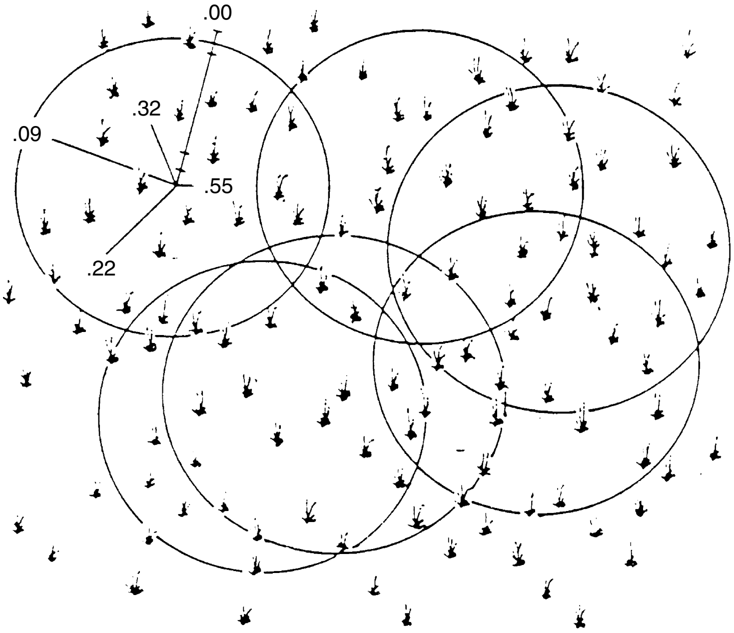


*Figure 3-4.* Spatial model of *Agropyron spicatum*. Circles represent inherent units of ecological scale. Any point of the landscape is the center of a natural scale unit. The distance from each center is measured and when the correlation declines to zero it indicates the bound of the inherent unit of scale (from Carlile et al. 1989, with permission).

## 3.7 THE IMPORTANCE OF THE PARAMETERS AT THE DIFFERENT SCALES

Some variables cannot change scale but it is their importance that changes. In this way, to predict the rate of decomposition in the soil means to know the environmental variability, the microclima and the characters of the litter. At a regional scale, temperature and humidity are good predictors of the decomposition rate.

The evapotraspiration is controlled at the leaf or tree scale by the deficit of the steam and by the stomata processes, but at a regional scale is the solar radiation the environmental variable.

The rate of mortality of oaks at a local scale has been found to decrease with increase in rainfall. At the regional scale, this mortality is lower in regions with more aridity.

## 3.8 GRAIN SIZE AND SCALING

Individuals can perceive the environment as coarse or fine grained according to the inherent characteristics. Generally, plants and other sessile organisms that spend most of their lifetimes in the same place have a coarse-grained perception of the environment.

However, when we distinguish competition processes for dispersal, it is possible to recognize different scaling factors in sessile organisms also.

Stratton (1995) has conducted an elegant experiment on variation in fitness of *Erigeron annuus*. This species show genotype-environment interactions on small spatial scales, although the evidence of such mechanism at 10-20 cm has been confirmed at 3-m intervals in only one experiment (1995) but not in the experiment conducted by the same author in 1994 (Stratton 1994). In this plant, competition appears at 20 cm distance and at 3 m the process of dispersal appears (Figure 3.5).

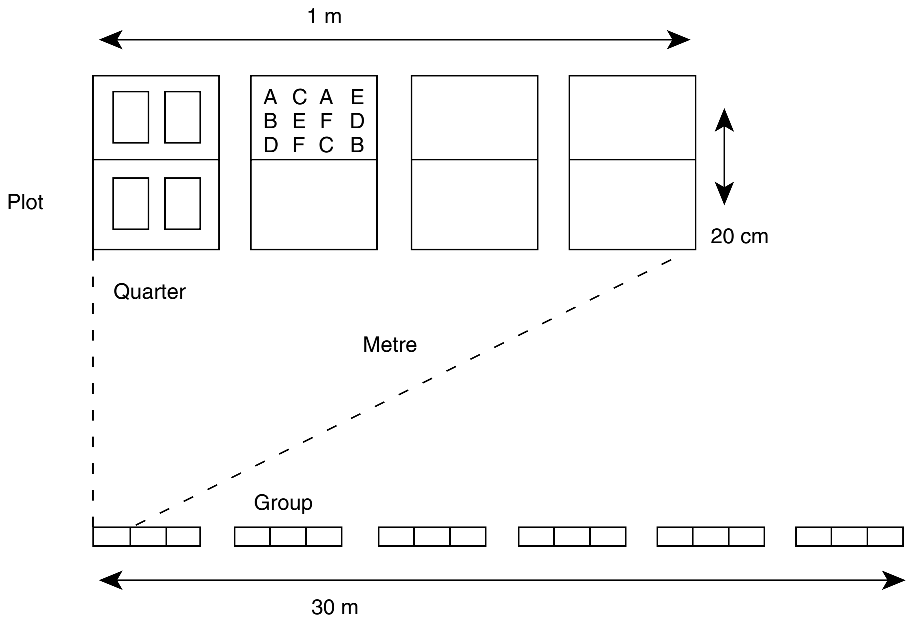


*Figure 3-5.* Experimental design of spatial arrangement of eight genotypes of *Erigeron annuus*. A transect of 30 m was divided in 6 groups, 3 m long and separated by a 2-m gap. Each group was divided into 3 quarters. Each quarter was composed of 2 plots. Every plot was subdivided in to two sub-plots of 5 × 10 cm. Every genotype was planted in each sub-plot. Two transects (10 apart) were selected (from Stratton 1995, with permission).

## 3.9 ASSESSING LANDSCAPE SCALE OF ANALYSIS

The scale is defined as a spatio-temporal dimension that produces the best information in the most efficient and unbiased way (Carlile et al. 1989). Wiens (1986) and Wiens et al. (1986) have argued that to study the interspecific competition, the more appropriate scale should be the local or regional but not the biogeographical scale.

In a theoretical sense, the best scale should be achieved using a hierarchy of scales having the capacity to correlate abiotic, biotic and human processes (Krummel et al. 1987).

According to Morris (1987), the selection of a scale should take into account the biological attributes of a species, like the home range, population density, dispersal movements, etc. In this way, the human scaling biases would be removed. Efficient sampling of landscape characters often requires splitting the investigation into scaled context: macro and micro habitats, that represent the grain of resolution (Figure 3.6).

When landscape studies require different aggregations of data it often becomes difficult to select the right dimension at which patterns are visible and related to processes. The effect of the changes of scale on the results is often underestimated or not easily detected. For instance, remote sensing data actually available are mostly based on four main sources with different resolutions:

| | |
|---|---|
| SPOT | 20 × 20 m |
| Thematic mapper | 30 × 30m |
| MSS | 80 × 80 m |
| AVHRR | 1 × 1 km |

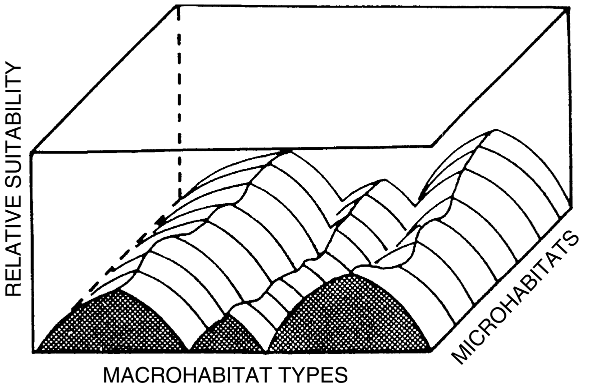


*Figure 3-6.* Macro and micro scales to measure habitat quality. Using a coarse approach, we can observe different macrohabitat variability across a spatial distribution. A fine resolution uses the habitat quality and micro-site that are recorded (from Morris 1985, with permission).

To understand what happens when we move from one resolution to another is absolutely imperative. Qi &Wu (1996) have tested three spatial autocorrelation indices (Moran Coefficient, Geary Ratio and Cliff-Ord statistic) to the topography and biomass of Peninsular Malaysia in 1992. They found relevant effects on results by changing scale for all the three indices. This means that for some attributes of the landscape there exist some threshold levels (e.g., for elevation) but this is not true for biomass that seems less sensitive to the scale of resolution. The influence of different spatial scales has been studied by Fuhlendorf & Smeins (1996) on the dynamics of common curly mesquite (*Hilaria belangeri* (Steud.)) Table 3.2.

Large scale is characterized by low variation between sampling units, high variation within units, high predictability or equilibria state. At a small scale the variation between units is high, predictability is low and there are no indications about the potential evolution toward a stable or chaotic behavior.

When we study landscape patterns, the choice of the resolution and extent are of fundamental importance to reduce biases. Thus, O'Neill et al. (1996) suggest that grain should be 2 to 5 times smaller than the spatial features of interest and that the sample area must be 2 to 5 times larger than the landscape patches, so as to avoid bias when indices of landscape structure like dominance, shape, contagion, etc., are applied.

## 3.10 EXAMPLES OF SCALES IN LANDSCAPE AND IN ECOLOGY-RELATED DISCIPLINES

### 3.10.1 Scaling the quaternary landscape

Most of the recent history and development of landscapes are strictly connected with human evolution. In particular, during the last 10,000 years, humanity and the landscape have evolved closely with feedbacks between

*Table 3-2.* Temporal dynamics of a grassland community dominated by common curly mesquite (*Hilaria belangeri*) according to different spatial scales (from Fuhlendorf & Smeins 1996, with permission)

| | *Scale* | |
|---|---|---|
| | *Large (exclosure)* | *Small (quadrat)* |
| Variability between unit | Low | High |
| Variability within unit | High | Unknown |
| Potential predictability | High | Low |
| Probability of equilibrium | Possible | Minimal |
| Probability of chaos | Minimal | Possible |
| Event of driving process | Large | Small (variable) |

natural and human-driven processes. For this reason, the history of the recent past assumes a special value in landscape ecology. The changes in structure and functioning of landscape from the hunting and gathering time (proto-history) to the discovery of agriculture and the birth of permanent settlements have affected most of our living realm (Figure 3.7).

Delcourt & Delcourt (1988) define four levels of the scale related to landscape ecological issues to study the quaternary landscape ecology:

Micro-scale dominion. This scale considers a time lag from 1 to 500 years and a space from $1m^2$ to $10^6$ $m^2$. Scientists working with this scale are geomorphologists, plant succession and animal ecologists and planners.

Disturbances like fires, wind throw and clear cutting are interesting at this scale.

Geomorphic processes as soil creep, movement of sand dunes, debris avalanches, slumps, fluvial transport and exposition, cryoturbation and biological processes are characterized by cycles of animal populations, gap-phase replacement in the forests, succession after abandonment.

In forested landscape fragmentation, increase of ecotones and change in corridor availability.

Mesoscale dominion: the mesoscale dominion extends from 500 yrs to 10,000 yrs and in space from $10^6$ to $10^{10}$ $m^2$. In this period are the events that range from the last interglacial interval and on a space from the watershed on second-order rivers. In this domain, the cultural evolution of humanity occurs.

Macroscale dominion: the macroscale dominion extends from 10,000 yrs to 1,000,000 yrs and with spatial extension from $10^{10}$ to $10^{12}$ $m^2$. In this dominion, the glacial-interglacial cycles occurred and speciation and extinction operated.

Mega-scale dominion: this dominion extends from $10^6$ yr to 4.6 billion years, with an extension $>10^{12}$ $m^2$ covering the American continent and interacting geological events like the plate tectonics movements.

### 3.10.2 Scaling patterns: The catchment scale

This scale is very popular in this period. The catchment scale that pertains to terrestrial and aquatic ecosystems, recently reviewed by Hornung & Reynolds (1995), seems to be a very promising dimension in which the fluxes of water and elements link the different components of the systems. Disturbance regimes such as agricultural intensification, afforestation and fires can be monitored using the chemical composition of streams and underground and surface waters.

Especially small catchments can be adaptable components to study pollution, land management activity and environmental changes. The possibility to increase spatial and temporal resolution is a further possibility to investigate in greater depth.

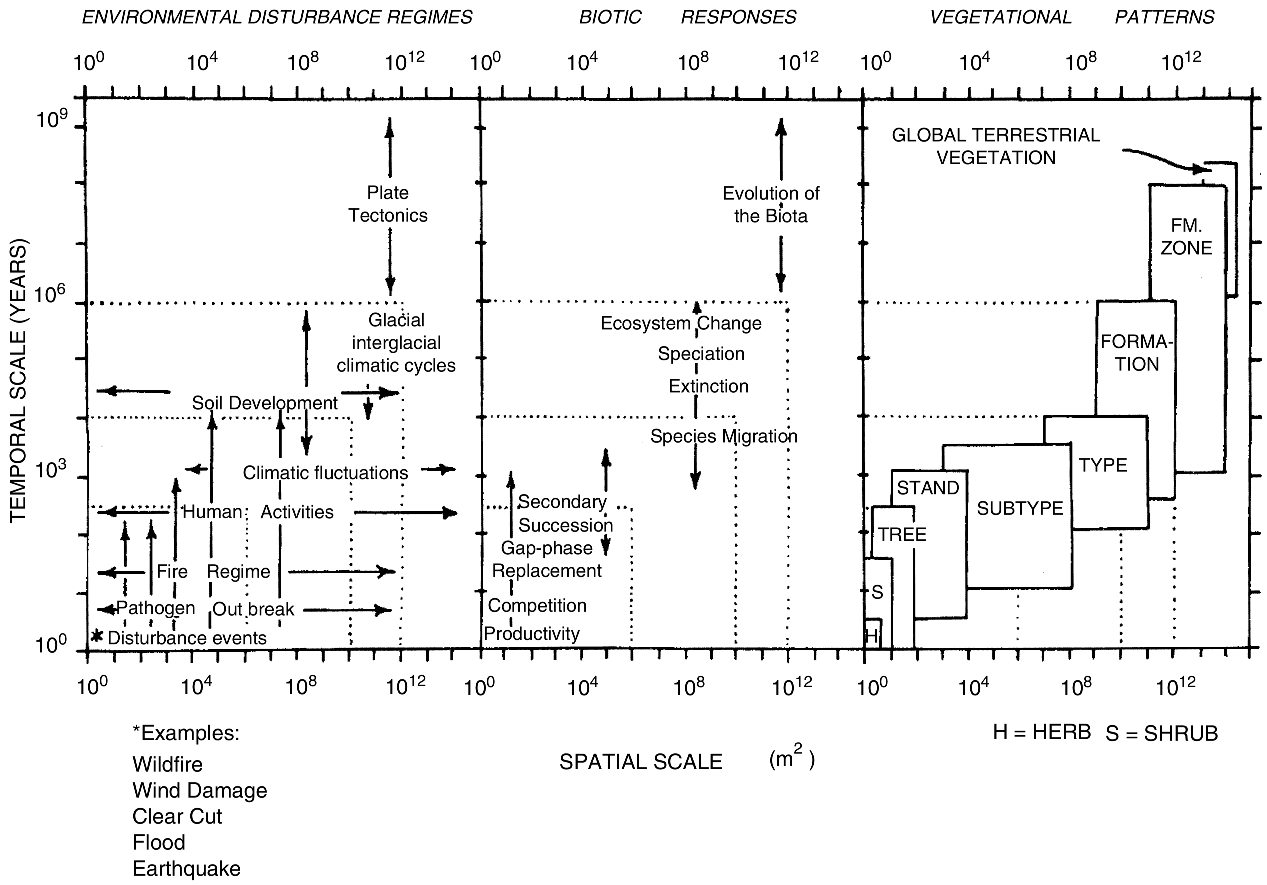


*Figure 3-7.* Effects of different disturbance regimes, biological responses and vegetational patterns in three spatio-temporal domains (from Delcourt & Delcourt 1988, with permission).

### 3.10.3 Scaling abiotic processes: Hydrological processes and scales

Hydrological processes are principal components of landscape mechanisms. Their dynamics have a dramatic influence on most of the abiotic and biotic processes. They range in eight orders of magnitude in space and time occurring at a wide range of scales from unsaturated flow 1 m soil profile to floods in river systems of a million square kilometres, from flash-floods lasting some minutes to flows into aquifers over hundreds of years (see Bloschl & Sivapalan 1995 for a review) (Figure 3.8).

Usually, three levels of scale are used in the study of hydrological processes: (a) the lifetime (duration) (for an intermittent process like a flood); (b) the period or cycle (for a periodic process like snow-melt; and (c) the correlation length (integral scale) that represents the average distance of correlation between two variables.

In hydrological studies that are basic components of the functioning of a landscape, the space scale ranges from 1m (local scale) to hill slope (reach) (100 m) to catchment scale (10 km), to regional scale (1000 km).

We have three levels: the event scale (1 day), the seasonal scale (1 yr) and long-term scale (100 years) (Figure 3.9).

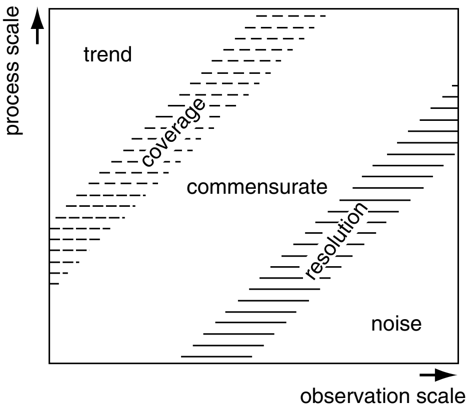


*Figure 3-8.* Plotting the process scale with the observation scale creates three regions in the design according to the sampling resolution. If the coverage is smaller than the process measured, the information achieved can be described as a trend. On the other hand, if the process is smaller, then the resolution appears as noise. The intermediate belt appears as a commensurate space (from Bloschl & Sivapalan 1995, with permission).

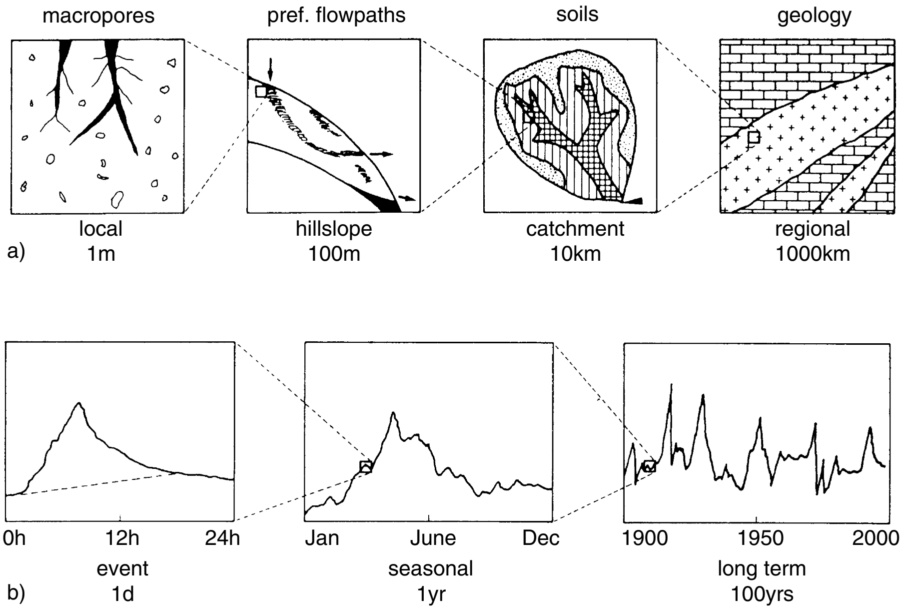


*Figure 3-9.* Components of catchment and hydrological processes across spatial and temporal scales (from Bloschl and Sivapalan 1995, with permission).

### 3.10.4 Scaling evidence in animals

Every species perceives the surrounding environment (landscape) in a different way. The movement of a grass stem appears parrossistic for aphides but is not perceived at all by deer.

A landscape homogeneous for a species, as a mountain prairie for water pipits (*Anthus spinoletta* (Motacillidae, Aves)), is perceived to be heterogeneous for the *Erebia* (sp.) butterfly (Satiridae, Lepidoptera) that distinguishes in these prairie patches different food resource availability.

Unfortunately, we often select scales more comfortable to our metrics than to the species (Dale et al. 1989; Wiens & Milne 1989, Wiens 1992), although it is possible to judge the best range of scale at which an organism spends its life (territorial behavior, dispersal movements, food research) (O'Neill et al. 1988).

The animal behavior interacts with the environmental patterns and processes across several spatio-temporal scales (Gardner et al. 1989).

The fact that organisms have capacities to move across a range of scales is well documented. This capacity is important, considering the complexity of the life cycles of organisms such as mammals.

Dorcas gazelles (*Gazella dorcas*) foraging in the Negev desert (Ward & Saltz 1994) select a plot with a high density of madonna lily (*Pancratium sickenbergeri*). In this plot, at a small scale they stay longer compared to a random walk model. But at broad scale, they move directly from one plot to another, suggesting that this species samples the environment repeatedly.

Many organisms are selected as bioindicators. They must have the requisite to be independent of the chosen scale. To test this hypothesis, Weaver (1995) studied an arthropod community across a range of four spatial scales, each scale nested in the others. He found that the proportion of species in a sample depended on the scale of observation. But Acari and Collembola richness showed a decrease of richness, increasing the scale of sampling presenting a uniform distribution in the soil. The diversity of Aranaceae, Thysanoptera, Formicidae and Coleoptera larvae increased with the addition of new samples. Especially Coleoptera added new species from 4% in a sample to 22% of total species moving from samples (n. 93), plots (n=24) to stand (n=4). This means that these species are patchily distributed and also perceive the environment as patchy. Diptera larvae remained constant across the sample scale. These data are relevant in a perspective of monitoring biodiversity. If, for many groups, richness is a matter of spatial scale to improve monitoring efficiency, the spatial scale of sampling seems to improve the inventory efforts.

For instance, Roshier et al. (2001) have found that the driest parts of Australia have the highest richness of water birds. They argued that in respect of the human scale, perception of local water availability, birds that have a wider capacity to perceive more connected and suitable habitats that are apparently isolated (Figure 3.10).

### 3.10.5 Landscape organization and scaling approach

It is a common practice to superimpose a map of emergent characters of a land mosaic (heterogeneity) with the map of distribution of organisms or their emergent characters like diversity. This exercise is full of uncertainty and biases. Recently, Ernoult et al. (2003) have proposed a new approach to create a more consistent methodology to evaluate the degree of relationship between species and their environmental context. Two measures of landscape organization are proposed: the alfa organization and the beta organization. Alfa organization measures the degree of deviation from random distribution of the selected feature (such as land use). Beta organization measures the degree of deviation of a spatial distribution of a property like land use (see the chapter on methods for more details).

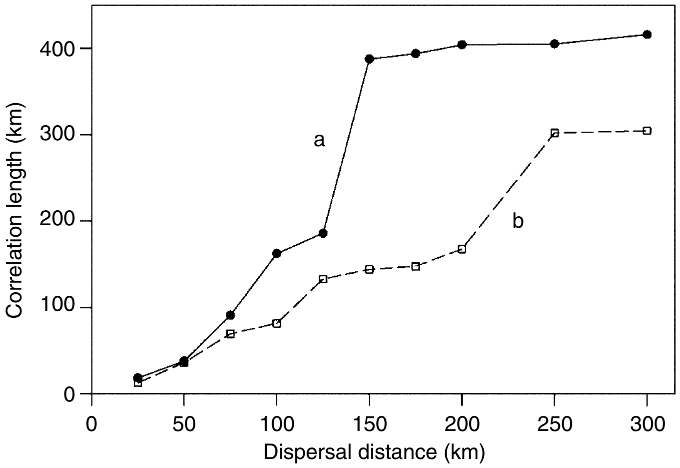


*Figure 3-10.* Wetland connectivity and dispersal distance that a water bird could move between adjacent wetlands: (a) after a small wetland-filling rainfall event in March 1987; and (b) three months later when distribution and number of wetlands was reduced (from Roshier et al. 2001, with permission).

Low values of alfa and beta organization indicate a random distribution of potential resources for organisms, and a less metastable system. The modern use of land by agriculture is less coupled with soil type, water availability and nutrient distribution because all are supplied artificially. The result is a system less stable and unable to support organisms operating at the scale at which humans use the land.

The perception of the surroundings by birds changes according to the species considered. Howell et al. (2000) have observed that in midwestern forests, 29% of bird species is most sensitive to local vegetation variables (number of living stems, organic litter depth, percentage of canopy cover, estimated percentage of forbs) while 67% was more sensitive to landscape variables (forest cover, cover area, edge density and mean patch size).

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## Chapter 4

# EMERGING PROCESSES IN THE LANDSCAPE

## 4.1 INTRODUCTION

This chapter focuses mostly on processes operating in a landscape across a broad range of spatio-temporal scales and which, in turn, influence many landscape patterns. Landscape is often investigated from the perspective of patterns (see Chapter 5) but it is also a dynamical earth surface system, in which instability creates sensitivy mosaics with the possibility of rapid irreversible changes of the entire system due to perturbations (Thomas 2001). Perturbation that occurs at a small scale cannot change the stability of the system, but if this perturbation occurs at a larger scale, the system can abruptly react by changing. For instance, in the cycle erosion/sedimentation, many landslides are the result of crossing of an internal threshold of soil stability, after a long-term accumulation of small perturbations. New organization after a perturbing event can be propagated in space like the gully erosion of sediments (Figure 4.1). The behavior of the landscape appears in many cases nonlinear, and self-organized. Critically, we have already seen the landscape to be a complex system.

Among the huge number of processes acting in a landscape we have selected the more pre-eminent and widespread, on which we have enough information (Disturbance, Fragmentation, Connectivity and Connectedness, Corridors, Flux of water and nutrients in soil landscape). The framework produced by this analysis is not uniform or homogeneous, reflecting the gaps in research and diversity in conceptual and operative approach and has to be considered a simple introduction. The strategy that we have utilized in distinguishing these processes is the result of an approach used to describe in a

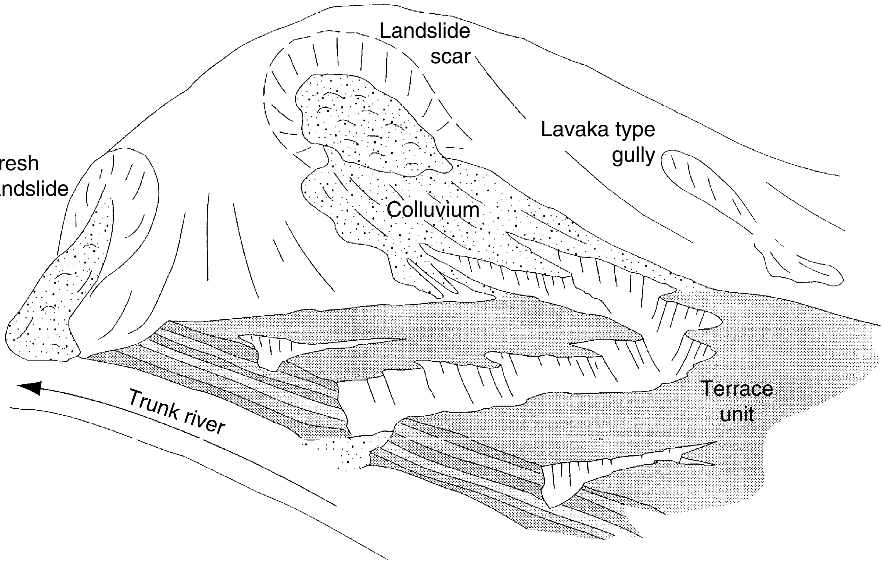


*Figure 4-1.* Landform elements along a sensitive land mosaic cycle. After a landslide, colluvial sediments are eroded along a river bank (from Thomas 2001, with permission).

simplified but in a more understandable way the emerging components of landscape complexity.

Most of the processes described in this chapter are related to each other. Disturbance and fragmentation are two processes with strong relationships and it appears hard to distinguish the role and the rate of the interactions. These two processes are mainly responsible for heterogeneity in the (landscape) mosaic. These processes have effects and relationships with many other abiotic and biotic processes according to different hierarchical levels of functions and patterns. Disturbance occupies a pre-eminent position in landscape functioning and is the main process responsible in shaping landscapes and their components. This process is driven by many factors and interacts with other processes acting in a more restricted context like fragmentation or land abandonment. In some cases it becomes hard to distinguish the pattern from the process role, as in the corridors. These objects may be structures (a road) or may assume the role of functional "invisible" roads (the migratory routes of birds and butterflies).

## 4.2 DISTURBANCE

### 4.2.1 Introduction

Disturbance is a very common and widespread phenomenon in nature and may be defined as a discrete event along time that modifies landscapes, ecosystems, community and population structure, changing the substrate, the physical environment and the availability of resources (White & Pickett 1985). It can be considered as a basic process, responsible for many other processes like fragmentation, animal movements, local and regional extinction, etc.

Every landscape is shaped, maintained and/or changed by disturbance. For instance, disturbances like clear cutting and wildfires have a strong influence on the structure and functioning of many landscapes.

Disturbance is very common in different systems, working at all spatio-temporal scales producing an alteration of resource availability and of the structure of the system. Disturbance occurs in many biotic assemblages, at all levels of organization from individual to landscape. Disturbance combines long-term scale changes with "actuality". The basic variables of disturbance are magnitude, frequency, size and dispersion (Figure 4.2).

To predict the impact of a disturbance regime on communities and landscape, it is necessary to understand at least the spatial and temporal architecture of the disturbance, as posited by Moloney & Levin (1996). Disturbance is a source of spatial and temporal heterogeneity. At the landscape level, disturbance is related to patch structure and spatial arrangement,

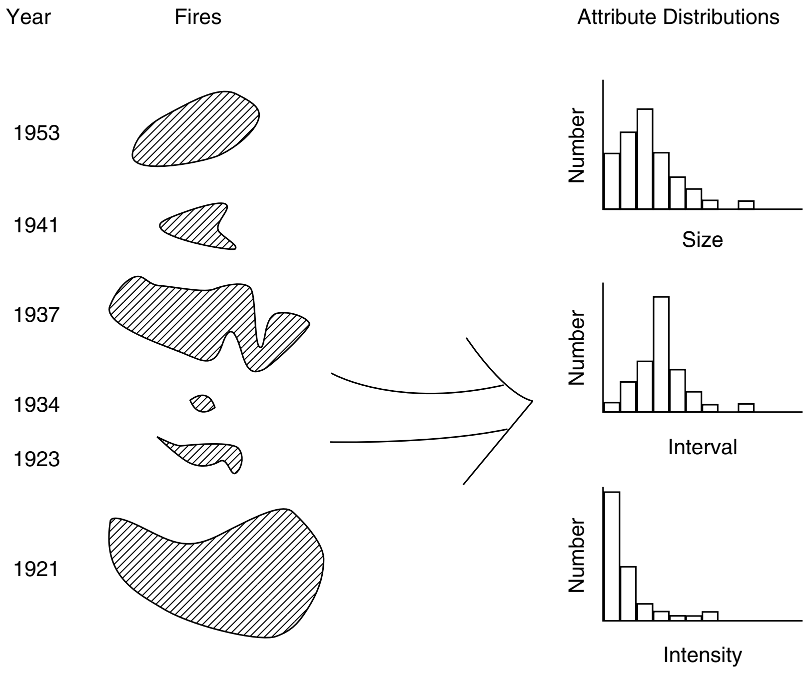


*Figure 4-2*. Example of fire disturbance regimes during a recent period. Every disturbance event, in this case fire, has a disturbance patch with different shape and attributes (size, interval and intensity) (from Baker 1992, with permission).

determines the fate of patches, their size and duration. Severe disturbances or the lack of disturbances generally have depressing effects on the diversity. Intermediate disturbance seems to enhance diversity in the systems. Where disturbance recurs more frequently than the time required for competitive exclusion, the diversity of the biological assemblage is maintained. It is the case in montane meadows in which human disturbance regimes by Summer hay harvesting and late Summer and early Autumn grazing prevent the development of a dominant species and, as a consequence, the floristic diversity is maintained at higher levels compared with less disturbed prairies. This system appears to be extremely fragile and needs external input to be maintained. We shall discuss the fate of such landscapes in greater detail in the chapter devoted to land abandonment.

Disturbance may be produced by abiotic factors such as solar energy, water, wind, landslides or by biotic elements like bacteria, virus, plant and animal competition, etc. We have dedicated a modest space to disturbance because the components of this process are described in other chapters, focusing on landscape dynamics. According to different disturbance regimes, the landscape can be deeply influenced. Gluck & Rempel (1996) have compared the landscape pattern of two forested areas of Northwestern Ontario subjected to clearcut and wildfire respectively. Patches of clear cutting were found to be larger in size and with more irregular edges and more core areas than those in the wildfire landscape.

When an infrequent event like a large fire which occurred in the Yellowstone (USA) landscape in 1988, changes in floristic and vegetational structure can occur. This is the case with aspen seedling recruitment which represents a substantial change in the landscape, although long-term fate of this post-fire recruitment cannot be predicted at present (Turner et al. 2003).

Before the European settlement of North America, fires produced by indigeneous dwellers or by spontaneous causes occurred more frequently than suspected, shaping landscape mosaics and driving soil nutrients. For instance, in eastern deciduous forests, after the intensive logging for charcoal production during mid and late 1800s for the iron industry, most of the forests experienced a secondary succession for at least a century, fire suppression for half a century and chronic atmospheric deposition. The combinations of these factors has varied the structure and composition of such forests. Recently, in order to restore a forest dynamic and to reduce the effect of atmospheric deposition, a long-term program of prescribed fires has been launched with controversial results, as argued by Boerner et al. (2000). The use of prescribed fires as a regular practice to restore ecosystem functionality is more than a promise, requiring a lot of local information about the natural history of the burned site and a precise long-term protocol for interventions.

### 4.2.2 Snow cover, an example of abiotic disturbance

Due to the high climatic constraint, the vegetation cover in alpine-type landscapes is extremely patchy. Snow cover controls the distribution of many species of plants, reducing the length of the growing season. The distribution of snow is strongly conditioned by topography and wind patterns. But exposed ridges experience low temperature in winter and animals like moles, gophers, voles, etc., responsible for the fine-scale mosaic, are also conditioned by snow accumulation. These species find refuges in snow accumulation and protected trails for soil exploration. In winter, when the soil is covered by snow (Figure 4.3), the snow vole (*Microtus nivalis*) often builds its nest with dry grasses and moss on the surface of the soil and digs tunnels in the compacted snow to search for food.

Plants react to snow cover in different ways (see Walker et al. 1993 for more details on plants of the Rocky Mountains). Some species escape deep snow cover (for example, *Paronychia pulvinata*), others are mainly localized in deep snow cover (for example, *Sibbaldia procumbens*) and others show no precise snow interaction, spanning a broad range of snow depth.

These plants are good indicators of plant association and, therefore, can be used as indicators of landscape scale plant community distribution.

Snow accumulation has an indirect effect on vegetation and the circulation of nutrients in the soil during the spring snow melt. This process is extremely

*Figure 4-3.* Snow accumulation during wintertime in soil depressions creates temporary habitats for micromammals such as snow voles (*Microtus nivalis*) (M. Cavalbianco, northern Apennines, Italy, 1800 m a.s.l.). The patchy distribution of these accumulations influences vegetation, especially in springtime, due to the different soil temperature and water content.

important in alpine regions, where plants suffer from nitrogen and phosphorus deficits (Figure 4.4).

### 4.2.3 Human disturbances

Human disturbance is not really different from natural disturbance but with some significant differences, especially in extension, severity and frequency. These last factors make all the difference (Figure 4.5).

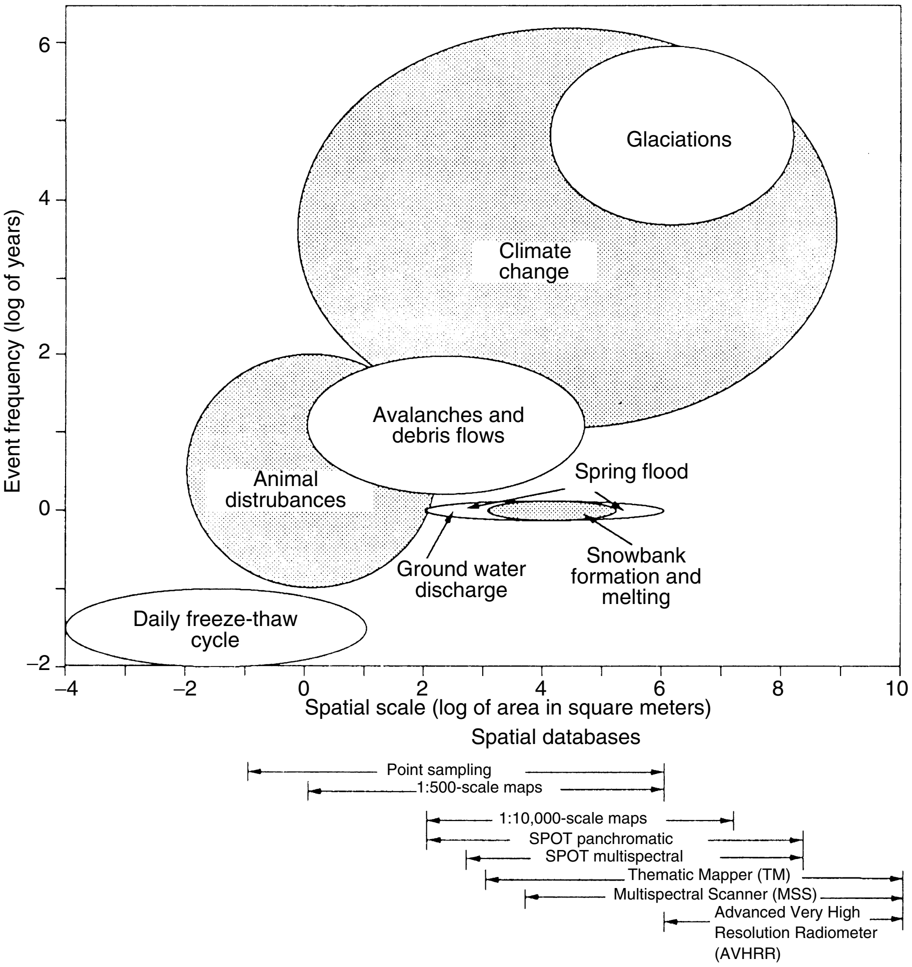


*Figure 4-4.* Frequency of the disturbance and the spatial scale of resolution in cold climates. The available data types are indicated at the bottom of the figure as examples of the application of a multiscale approach ranging from data input by field survey (quadrat plots) to remote sensing techniques (Advanced Very High Resolution Radiometer, AVHRR) (from Walker et al. 1993, with permission).

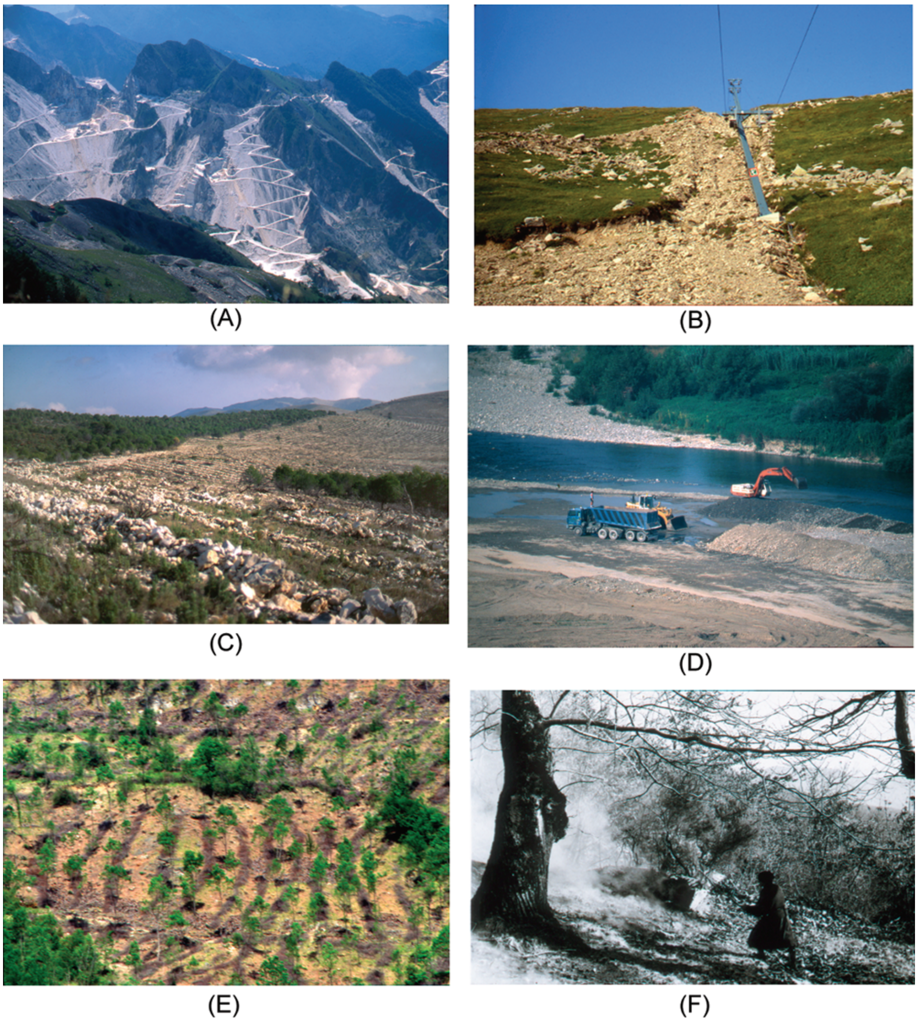


*Figure 4-5*. Human disturbance may be caused by different types of acitivities:(a) mining (Alpi Apuane marble mines), (b) recreation infrastructures (sky facilities) or (c) restoration of plans that are not ecologically oriented ("ploughing" in an arid-rocky mountain landscape in South Spain, that are improved a pine plantation). (d) gravel mining in active river beds (Aulella river, 1990 Aulla), (e) coppicing, "matricinato" selective cut (Northern Apennines), (f) prescribed fire in sweet chestnut orchard. All these activities due to the severity of the disturbance (a,c) or the fragility of the ecosystem (d), cannot be incorporated in the landscape.

Forestry, agriculture, development, infrastructures are some of the disturbances that human activity can produce on the landscape and at larger scales in regions. Human-environment interactions are distributed world wide and we can emphasize that all parts of the planet are affected by such a dominant presence. Naveh (1992) utilizes the term "total human ecosystem" referring to the Earth. The disturbance regime due to human activity is expanded by technology to a broad range of spatio-temporal scales, with effects ranging from the deepest oceans to the highest mountain ridges. The capacity of the landscape to incorporate human disturbance is in many cases outside the limit and disturbance processes are transformed into stressful processes, which reduce the diversity of the ecological communities.

In some cases, human disturbance has multiplicative effects both on landscape patterns and population dynamics. An example is from stream ecology. Streams have longitudinal as well as lateral dynamics, influenced by the watershed quality and in-stream modifications. Fishes living in such habitats are size-structured vertebrates. This means that a population is composed of differently aged individuals with a broad range of sizes. For every size class the provided habitat is specific. Any alteration of stream structure has a specific effect on the different age-classes of fishes. The alteration of stream dynamics and structures by human use of the land produces consistent effects on the composition of fish populations. For instance, a disturbance of the mainstream for gravel mining can reduce the depth of water-removing habitat for large-sized fishes and, conversely, can increase the abundance of small-scale individuals by offering shallow waters. As pointed out by Schlosser (1991), alteration in structural and functional relationships inside the landscape can reduce the diversity of adult and juvenile fish, decrease complexity in the size structure, increase the abundance of juveniles because of increased area of shallow refuges and also increase the variability in fish abundance.

Deforestation for logging represents a major source of landscape disturbance, especially in relatively pristine areas. McGarigal et al. (2001) have described the cumulative effect of roads and logging in a wilderness area in the San Juan Mountains, Colorado. These effects, evaluated in the interval between 1950-1993, seem quite trivial on the scale of 228,000 ha landscape. At this scale, the landscape seems capable of incorporating disturbances, but at an intermediate scale 1000–10000 changes are evident. This study demonstrates that environmental evaluation is scale dependent and that a multiscale approach can overcome the difficulties of environmental assessment.

Often, a disturbance regime is the result of cumulative effects. For instance, in the Great Plains grasslands, largely converted into cropland, the remmant native grasslands have from 1965 to 1995 experienced a dramatic increase of *Juniperus virginiana* L. woodlands and of deciduous woodlands (Coppedge et al. 2001). This last cover largely depends on the juniperus encroachement. This fact has increased the fragmentation of the vegetation cover that appears more patchily distributed and also favored by the lack of wild fires.

Often, the attributes of the human disturbance differ from the attributes of a natural disturbance. For instance, a fire along a Mediterranean coast produced intentionally or by human "lack of attention" is not different as a process from a wildfire, but this fire, if repeated at every season (improbable in wild conditions), can produce stress on vegetation, reducing vegetation, cover, increasing soil erosion, etc.

Human activity is modifying the face of the Earth, reducing natural vegetation, animal communities, and exemplifying landscape mosaic. The rearrangement of natural systems according to human needs, especially if carried out by burning fossil oil, dramatically interferes with the ecosystem dynamics and landscape mosaic structure (Palmer et al. 2004).

For instance, the increase of urban sprawl at the planetary scale affects the environment in several ways and at a multiple levels of biological organization. Recently, Blair (2004) has discussed the effects of urban development on birds in northern California and Ohio, at individual levels in terms of predation, that seems lower in urban areas (using artificial nets). At species level, invasion-extinction is strongly affected by different levels of local urbanization. At the community level, an urban area can have a diversity peak, where urbanization is moderate.

Human-caused disturbance has recently been considered by Frid & Dill (2002) as a form of predatory risk. In fact, there are several evidences that human activity produces a non-lethal disturbance on the behavior and the reproductive success of animals. Predatory pressure and disturbance produce similar trade-offs to avoid risks and perform other functions (activities) like feeding, mating or parental caring. Predatory avoidance is a function that requires energy and this activity reduces the energy available for other functions. Human activity disturbs wildlife in different ways, by producing loud noises like the shot of a rifle or the sound of a horn or the intrusion of visitors into the animal ranges. Landscape features can reduce the cost of this disturbance (predatory-risk hypothesis) by reducing the distance at which animals react, moving from a site and interrupting a function. For instance, animals like fallow deer (*Capreolus capreolus*), feeding at the ecotones, can feel safer if the ecotones have a convolute shape or if there are stepping stones like fragments of woodlots between forest and open grazing fields. The reaction to human disturbance largely depends on the physiological status of the animals. For instance, in some amphibians, safety is postponed for mating access. In a territorial display, European robins (*Erithacus rubecula*) reduces the distance from feral cats, dogs and humans. But organisms forced by the disturbance to select less favorable areas can experience a rapid decline in intraspecific competition or an increased predatory pressure.

Human disturbance can produce unexpected effects; for instance, it can facilitate the entrance of invaders into a community. This is the case of *Chaerophyllum aureum*, a species that is common in meadows in Pyrenean valleys. The genetic variability that is the main cause of diffusion of this species is increased by the human practice of hay production, as reported by Magda &

Gonnet (2001). These authors, using polyphenol compounds as individual markers, have found that in the studied area at least one dominant genotype and five different populations exist. The spatial arrangement of "genetic" populations was found independently by environmental factors but mainly due to human practices that the seeds of this plant are mixed by collecting hay and "amplify the colonization process of adapted genotyopes." Also, recreation is not a secondary disturbance for organisms like birds (see e.g., Bennet & Zuelke 1999).

## 4.2.4 Gap disturbance in forest

Gaps are small openings in forest cover due to local events such as tree fall and are not generally a random event, but some sites are more likely to have gaps than others (Poorter et al. 1994). Most of the species that live in old-growth

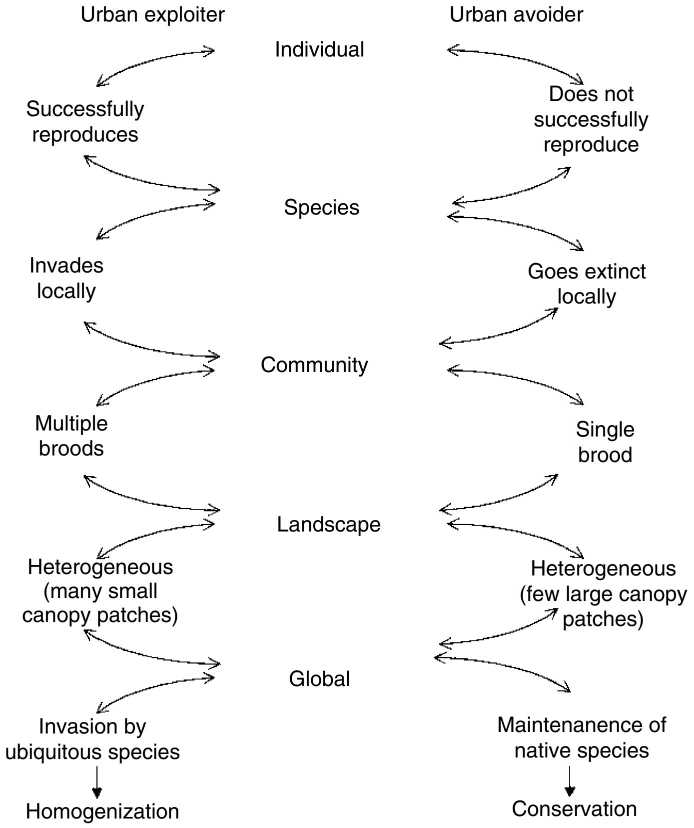


*Figure 4-6.* Conceptual model used to illustrate the relationships of birds at different levels of aggregation (from local to global) and the urban sprawl according to the attitude of species to exploit or to avoid an urban environment (from Blair 2004, with permission).

forests require gaps to reach maturity. Across the forest, the gap density is constant but these authors have found that along a catena, gaps are more abundant in the middle part, while in the upper and lower slopes, gaps are less frequent. The regeneration occurring after the formation of a new gap plays a fundamental role in structuring forests and maintaining species diversity.

Gaps are inhabited by different species of organisms in comparison to the forest understory. Large, infrequent blow-downs can modify the structure of forests favouring insect pests, secondary succession and fire propensity. Such disturbances produce only a partial loss of overstory trees, and most of the dead snags and fallen woody material is retained. Edges between blowdown and intact forests are typically lower-contrast edges. A study conducted by Lindemann & Baker (2001) on the effect of a Routt-Divide Blowdown (Northern Colorado in 1997), has demonstrated a wide array of patches produced by wind storm with an unusual variability in patch attributes (size, perimeter length, distance to the nearest patch).

Large forest disturbances such as hurricane Hugo can change the structure of bird assemblage in old gaps and new forest disturbances. Wunderle (1995) has found that the major effect of the passage of Hurricane Hugo on bird assemblage in a Puerto Rican forest has been the loss of distinctiveness between the bird assemblage living in the gaps and birds living in the disturbed understory. According to this author, probably many years will pass before the gap and understory become distinct in structure and resources.

In forests where large disturbances are rare, the gaps created by the killing of one or a few canopy trees plays a fundamental role in structuring the entire forest. Gaps are particularly evident in the changing phase from mature to old growth forests. A tree that dies is considered a “gapmaker” because it creates the gap. An edaphic gap has to be distinguished from a tree gap because it is produced by edaphic conditions such as stream courses or thin soils.

In the forests of British Columbia, Lertzman et al. (1996) have estimated that in the absence of a large disturbance such as fire, wind storm or insect diseases, gaps created by a regime of small-scale, low-intensity disturbances are responsible of the turnover of these forests in between 350 and 950 years. Where gap disturbance is common, interestinly, is about 56% of the forest area investigated. Most of the gaps are produced by more than one dead tree. Some gaps (a third) were found to be produced by edaphic factors like stream courses. Figure 4.7 reports the frequency distribution of edaphic gaps.

### 4.2.5 Gaps in savanna

Recently, Belsky & Canham (1994) have discussed the structure and function of savanna trees in a matrix of grasslands comparing forest gaps with savanna

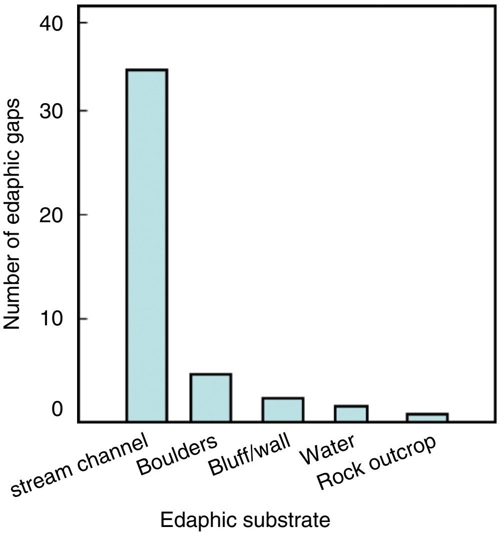


*Figure 4-7.* Frequency distribution of edaphic gaps distinguished by physiographic causes (from Lertzman et al. 1996, with permission).

trees. This approach seems very interesting, although in some cases, it is intriguing. Tropical savanna dynamics may be explained in terms of gap dynamics. Trees and shrubs are the "gap" in the grassland matrix. Figure 4.8 reports on an example of forest and savanna gaps (Belsky & Canham 1994). In savanna "gap", a gap is initiated by tree seedling establishment and growth. The physical conditions

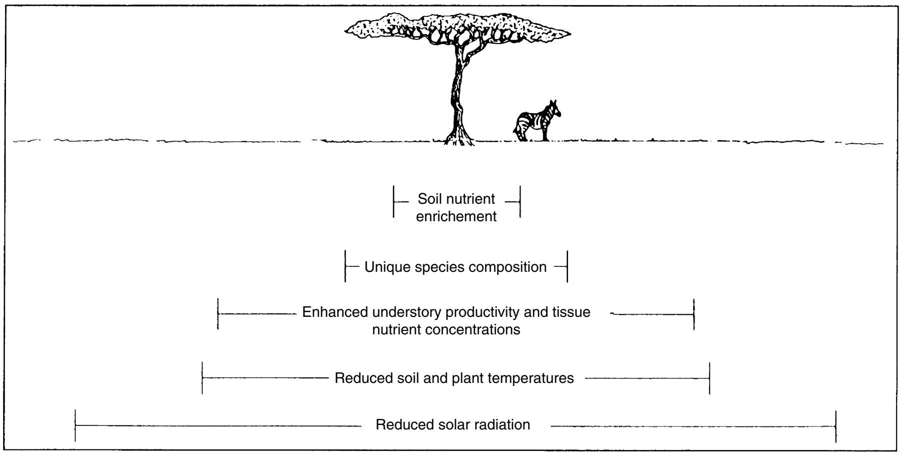


*Figure 4-8.* Effects of isolated trees in tropical savanna (*Acacia tortilis*) in Tsavo National Park, Kenya (from Belsky & Canham 1994, with permission).

under savanna trees are different compared with the surrounding open savanna, like gaps in a forest environment. During the wet season, the soil under the trees is dryer, but later in the season, the soil is wetter under trees due to reduced evapotranspiration in the shade and a cooler temperature. It is well known that under savanna trees, the soil is richer in nutrients due to root transportation, manure deposition by wild and domestic animals and by a less stressful bacteria cycle.

### 4.2.6 Fire disturbance in landscapes

Fire is one of the most important shaping agents in landscapes. It removes the undecomposed biomass and creates nutrient fluxes by ash deposit watering, contributing to the ecologically rejuvenating qualities in forest ecosystems (Moore 1996). In a dry continent like Australia, fires have played an important role in shaping vegetation mosaics and fauna distribution. In desert areas, fires produced by lightning create a complex mosaic of burned-unburned areas that favor several species of animals like lizards (Pianka 1986). Recent studies and simulations conducted by Haydon et al. (2000a,b) in the Great Victoria Desert have emphasized the role of wild fires as main perturbation agents. Fire size is influenced by wind direction, shaping scarring areas into an oblongate form. Perimeters of larger fires are more complex than smaller fires. Large fires have more tongues than smaller fires, according to the wind direction. Fire can be considered fractal objects (see Figure 4.9). In their studies, Haydon et al. have calculated that the return time is not less than 20 years and aproximately 2–5% of the area is burning each year. Older patches are more prone to burning due to a major accumulation of biomass.

Fire has been utilized as management tool to manipulate the ecosystem since Mesolithic times (Naveh 1990, 1991; Grove & Rackham 2001; Blondel & Aronson 1999). If the release of nutrients is well documented, the role of charcoal in the soil appears neglected. Charcoal has the capacity to retain water and a sandy soil can behave like clay if added to charcoal. But other functions have been recently recognized for charcoal as a sink for phenolic inhibitors. In this way, both plants and microbes are stimulated.

The effects of fires on vegetation cover depend on a plethora of concurrent factors like fire history (severity, recurrence), climate, topography and dominant type of vegetation. In Catalonia (northeastern Spain) Diaz-Delgado et al. (2002), using the Normalized Difference Vegetation Index from Landsat imagery, have observed that vegetation resilience calculated on the green biomass 38 months after the second fire increases with the time between consecutive fires (see Figure 4.10).

In the Mediterranean region, the fire regime actually has no possibilities to counterbalance the general trend of landscape coalescence, principally due to

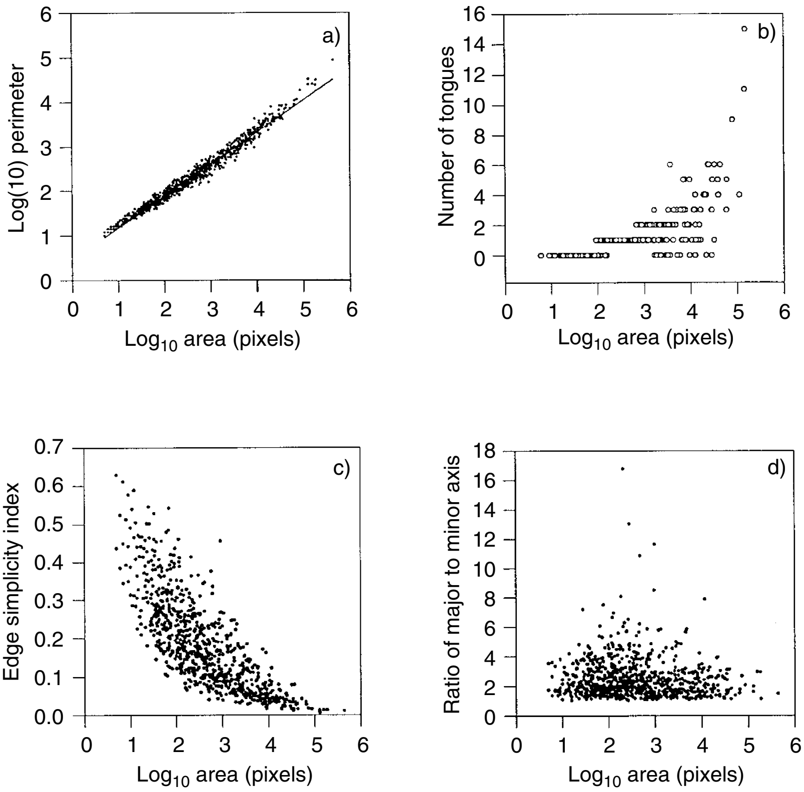


*Figure 4-9.* Relationship between area of fires and their shape (perimeter, number of tongues, edge simplicity and ratio of major to minor axis) of 817 fires (in B 341 fires were used) in the Great Victoria Desert, Australia, from 1972 to 1991 (from Haydon et al. 2000a, with permission).

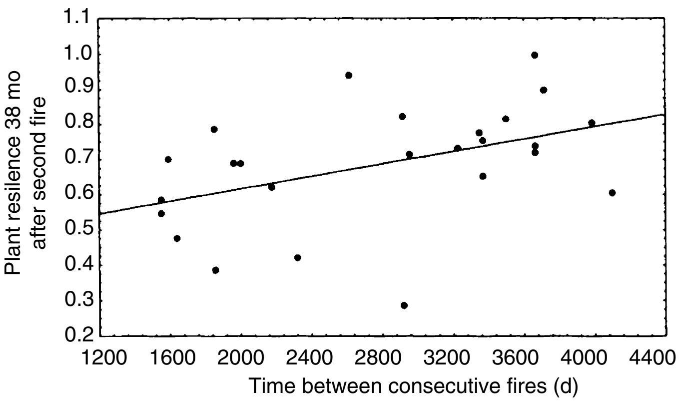


*Figure 4-10.* Relationship between cover resilience after a second fire (measured after 38 months from the last fire) and the interval between fires (from Diaz-Delgado et al. 2002, with permission).

*Table 4-1.* Implication of different scales of habitat dispersion on various attributes of fragments and fragmented landscapes (from Lord and Norton 1990, with permission).

| | *Geographical* | *Structural* |
|---|---|---|
| Size ($m^2$) | large>1000 | small<10 |
| Isolation | usually medium to large | usually small |
| Boundary gradient | steep | shallow |
| Impact of extrinsic disturbance | confined to edge and up to a few hundred meters | throughout |
| Vulnerability to functional disruption | medium to large | medium to small |
| Scale of organism affected | large generalist to medium specialist | medium specialist to small specialist |
| Advantages for conservation | usually has intact interior | usually greater total extent |

agriculture abandonment and shrubland increase. In Tivissa municipality (Catalogna, Spain), Lloret et al. ( 2002) (Table 4.2) have provided evidence, investigating the land cover changes in the period 1956–1973, that landscape heterogeneity decreases disturbance spread and that fires cannot reduce the actual trend of transformation of woody areas in shrublands. It seems that other drivers have to be found in the economic domain to explain the actual trend common to all southern Europe. Fire, when associated with grazing, can represent a dramatic disturbance in ecosystems. As reported by Bailey & Whitham (2002), large crown fires in Arizona affect aspen (*Populus tremuloides*) regeneration and arthropod species and abundance. These effects largely depend on fire severity and on elk grazing pressure. Fire severity *per se* has no direct effects on arthropod richness and abundance. But moderate

*Table 4-2.* Transition matrix of four dominant land covers between 1978 to 1993 in Tivissa Municipality, Catalogna, Spain (from Lloret et al. 2002, with permission).

| *Unburned areas (%)* | | | |
|---|---|---|---|
| | *from 1978* | | *to 1993* |
| | Dense forest | Open forest | Shrubland |
| Dense forest | 36.3 | 13.1 | 14.5 |
| Open forest | 2.4 | 1.6 | 1.4 |
| Shrubland | 48.4 | 77.2 | 78.3 |
| Agriculture | 11.4 | 6.2 | 4.2 |
| *Burned areas (%)* | | | |
| | *from 1978* | | *to 1993* |
| Dense forest | 16.4 | 9.4 | 8.3 |
| Open forest | 2.7 | 2.7 | 2.3 |
| Shrubland | 74.3 | 81.7 | 81.0 |
| Agricultural | 4.7 | 3.4 | 2.4 |

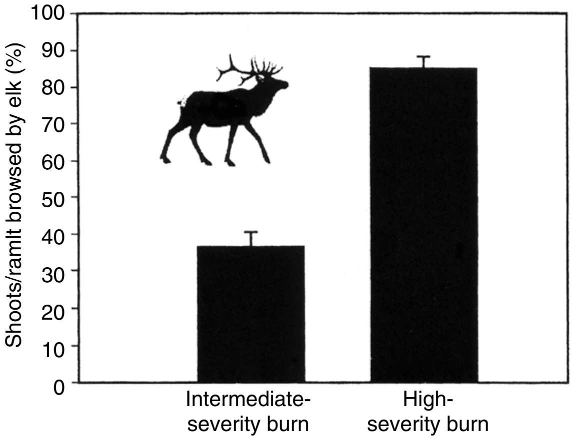


*Figure 4-11.* The severity of fire on aspen resprout is strongly affected by elk browsing. In high severity burn 85% of young aspen shoot are browsed by elk, but only 36% of shoots in intermediate burn site are removed by elk (from Bailey & Whitham 2002, with permission).

severity and moderate levels of elk browsing assure 30% greater richness and 40% greater abundance in arthropod communities. On the contrary, high-severity fires and high levels of elk browsing reduce diversity and abundance by 69% and 72%, respectively. The authors warn about the risk of depicting contrasting scenarios when disturbance elements are considered independently and stress the importance of having studies that incorporate greater complexity (Figure 4.11). In Brittany, Morvan et al. (1995) have observed that fire speed in heathland landscape is strongly linked to landscape heterogeneity, when a scale of resolution of 25×25 m is considered. The landscape heterogeneity increases with fire frequency but the diversity of growth decreases after one fire when fire disturbances occur frequently. The study of fire occurrences during a long period of time is reccommended by Rollins et al. (2002) as a historical baseline for fire management in wilderness mountain complexes. These authors have reconstructed the fire history of two wilderness areas of Rocky Mountains in New Mexico, Montana and Idaho during the twentieth century. Results indicate that the amount and horizontal continuity of herbaceous fuels is the limiting factor for frequency and spread of surface fires in the Southern Rockies. While the moisture status of large fuels and crown fuels are the limiting factors of the frequency of moderate-to-highly severe fires in the Northern Rockies.

Fire suppression has been a common practice during the second half of the twentieth century (see Figure 4.12). Such suppression has increased C storage in the soil and according to empirical and predicted data, fire suppression in the USA might represent 8–20% of the missing global carbon, as reported by Tilman et al. (2000).

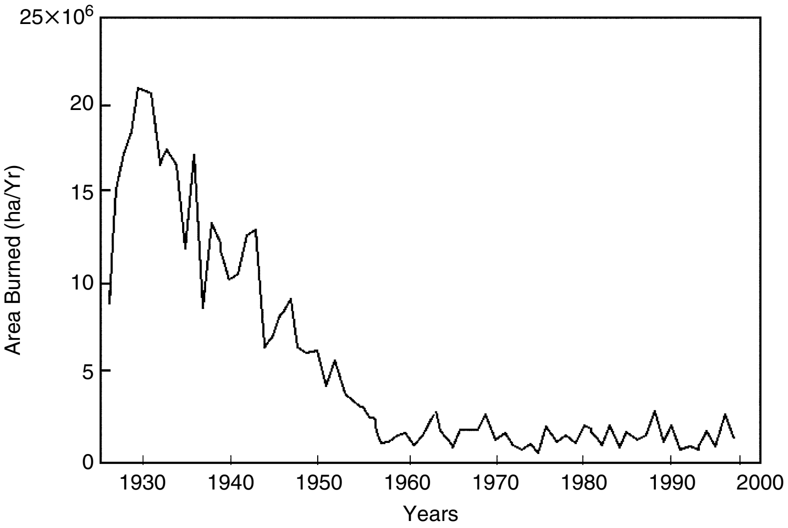


*Figure 4-12.* Trend of burned areas in the USA from 1926 to present (quoted by Tilman et al. 2000, with permission).

## 4.2.7 Pathogens disturbance

Less attention has been reserved for the role of pathogens in shaping and structuring forests. Pathogens influence forests at different ranges of spatial and temporal scale. Forest diseases occur in patchy distributions across the landscape (Lundquist & Klopfenstein 2001) and pathogens reflect their genetic variability and the landscape heterogeneity. This creates a disease-prone land mosaic across the entire forest landscape.

Some pathogens like *Brunchorstia pinea*, responsible for Scleroderris cancer in pines, are more active in cold temperatures, with more impact on stands occurring in topographic depressions and forest openings where the cold air accumulates. The cancer of sweet chestnut has accelerated the change of the landscape in the southern Europe, in combination with land abandonment. A great area occupied by this type of orchard has been modified in a short time by cutting off of diseased plants.

Pathogens play a fundamental role in the formation of gaps in mature and healthy old-growth forests. Patch-phase processes of disturbance create the conditions for landscape heterogeneity, enhancing plant diversity and resources availability for plants and animals. Pathogens also change the composition of forests, increasing the unevenness of stands. Knowledge of pathogen cycles is essential to an efficient and accurate management of forests (Castello et al. 1995).

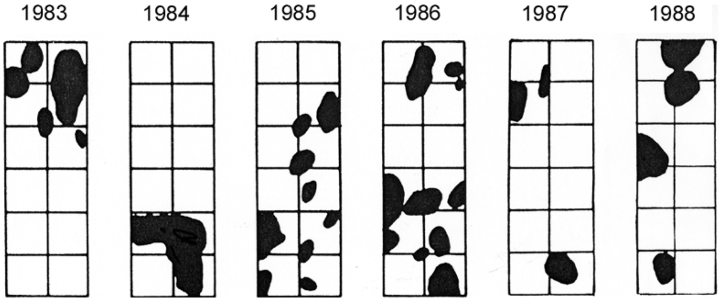


*Figure 4-13.* Spatial distribution of gopher disturbance by digging in a plot of 3x1 m from 1983 to 1988 in a serpentine grassland (from Hobbs & Mooney 1991, with permission).

### 4.2.8 Animal disturbance

Digging and grazing are the most common disturbances produced by animals (herbivores) (Figures. 4.13, 4.14, 4.15 and 4.16). This disturbance severely affects the distribution and structure of vegetation (grass, forb and shrubs). In forested area, grazing prevents the growth of seeds. Trampling associated with grazing modifies the composition of natural vegetation and reduces the interspecific competition creating patches of high diversity but this disturbance is often quite complex (Hobbs and Mooney 1991).

*Figure 4-14.* Terracettes associated with domestic sheep grazing in the M. Sillara, northern Apennines (Italy).

*Figure 4-15.* Ant nests in montane moorlands create disturbance patches, increasing the spatial heterogeneity.

In natural and livestock-grazed prairies, the deposition of urine is a cause of local disturbance that produces a complicated mosaic at a larger scale. This mosaic depends mainly on the density of grazing wild or domestic animals. Steinauer & Collins (1995) tested the effect of urine deposition in differently disturbed grasslands. Plant abundance increases after urine deposition but

*Figure 4-16.* Mole (*Talpa sp.*) are a disturbance agent in open and forested landscapes. Mound deposits are the center for seeding non-dominant plants.

α and β diversity displayed local behavior, mainly due to litter depth. This biomass accumulation attracts more herbivores and the effect of urine is expanded in the neighboring environment.

Finally, the grazing intensity in such patches has a much deeper effect than urine deposition alone. This seems a good example of disturbance overlap that can reinforce the reaction of the environment.

## 4.3 FRAGMENTATION

### 4.3.1 Introduction

According to different perspectives, fragmentation can be considered as the "negative image" of connectivity. These processes have a strong influence on the dynamics and fate of material and energy moving across a landscape.

Several papers have recently focused on the fragmentation processes as the central issue in landscape ecology and conservation planning (Saunders et al. 1991; Wilcove et al. 1986; Wiens 1994; Collinge 1996). Loss of native plant and animal species, invasion of exotic species, increase in soil erosion and decrease of water quality are some of the consequences of habitat fragmentation.

Fragmentation is one of the most severe world-wide processes depressing biodiversity. It moves at an alarming rate around the world, reducing large forest cover as well as natural prairies (Wade et al 2003). In some parts of the Earth, fragmentation has occurred mainly in previous centuries, as in Australia and in Brazil (Hobbs & Hopkins 1990) with devastating consequences on the environment (Figure 4.17). A recent investigation (Wade et al. 2003) has estimated that over half of the temperate broadleaf and mixed forest biome and about one quarter of the tropical rain forest biome have been fragmented or removed by human use. In boreal biomes, only 4% of the forest has been fragmented or removed.

Clear cuts and roads dramatically increase the fragmentation effects on forest cover, and especially roads are important agents of forest cover changes as argued by Tinker et al. (1998).

Fragmentation is a process that presents a negative influence on many species of plants, animals and ecological processes in landscapes as well as in seascapes (Hovel 2003). Reducing the size of fragmented blocks decreases the density of populations and meta-populations and the extinction risk grows, as is documented by Conner & Rudolph (1991) for red-cockaded woodpecker (*Picoides borealis*) populations in, eastern Texas. Fragmentation means geographic isolation and, after extinction, the probability of recolonization strongly depends on the distance of the fragments from the main core and on the quality of the surrounding habitat.

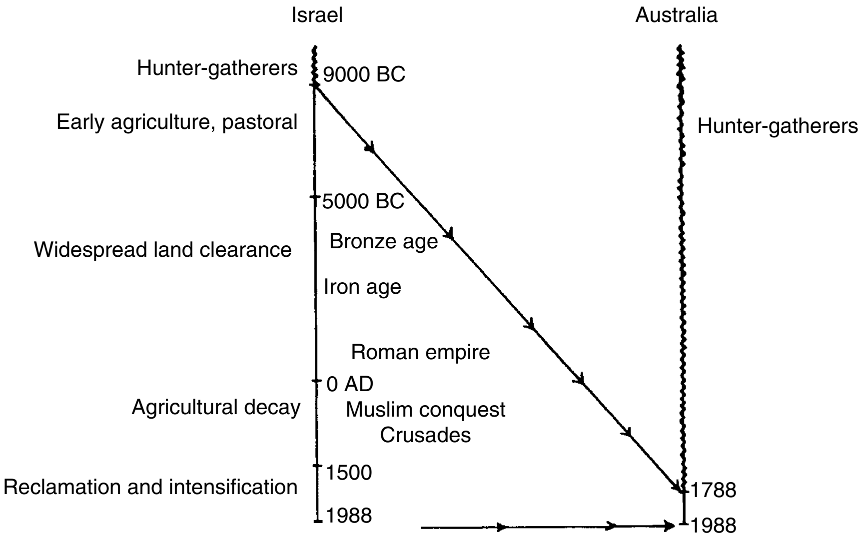


*Figure 4-17.* A comparison of the main modification of natural vegetation along the centuries in Israel and Australia (from Hobbs & Hopkins 1990, with permission).

Doherty et al. (2002), investigating residential birds living in forest fragments of different sizes, using a mark-recapture analysis technique in an Ohio agricultural landscape, have found that the survival rate was negatively affected by fragment size. Survival was higher in larger remnants and with adult birds. Severe winters strongly affect the survival but food supply in experimental plots have produced an increase in bird survival.

Zanette et al. (2000) have investigated the effects of fragmentation on forest-interior songbirds that are considered "area-sensitive" species because they are not found in small forest fragments. These authors have investigated the effects of forest fragmentation on the eastern yellow robin (*Eopsaltria australis*) living in two small (~55 ha) and in two large forest fragments (>400 ha) in a farmland mosaic in New South Wales (Australia), by counting the insect abundance and the reproductive success. Incubating females living in small fragments received 40% less food from males. The breeding season in small fragments was shorter; females laid eggs 7% lighter, and nestlings were smaller than the ones living in larger plots. This study confirms food shortage as the small fragment condition that affects the reproductive performance of this species.

In tropical areas, forest fragmentation affects pollen and seed dispersal, with modifications in gene flow (Hamilton 1999). Species sensitive to the edge (interior species) can reduce in abundance or in pairing success (Villard et al. 1993). Large predators disappear, producing outbreaks of foragers such as deer. This last effect allows further environmental degradation and disturbance.

Fragmentation is often interpreted by the general framework of the island biogeography theory (MacArthur & Wilson 1967) but area size and isolation factors taken into account by this theory are not enough to explain the effect of fragmentation in habitat islands. If the fragmentation is simply considered as the size of isolated patches, this approach appears to be uninformative. Fragments cannot be considered as true islands; in fact, the surrounding habitat is often not completely hostile to the species.

Other factors such as connectivity, presence of ecotones and corridors, and the metapopulation structure have to be taken into account, especially when fragmentation is studied on a landscape scale (Gu et al. 2002).

Fragmentation can be considered a continuum process, and according to a landscape perspective, matrix and patches are the elements that have to be used for considering a landscape, fragmented or not (Wiens 1994) (Figure 4.18).

Fragmentation is perceived in a different for the same species way according to the different species and also it may be different according to the season. Thomas (2000) has found that butterfly species with intermediate dispersing capacities are more affected by fragmentation in comparison with sedentary or highly-vagile species.

At the edge, the behavior of species is different. For some species, edges are highly suitable habitats, but others avoid them. Nest predation can be higher at the edges and this has a big influence on the suitability of the patches in a fragmented landscape (Pasitschniak-Arts et al. 1998). Fragmentation is really a dynamic process. The human disturbance regime as well as natural disturbances produce fragmentation but often the recovery of vegetation cover masks or mitigates this process. In other cases, the fidelity of some species to a site reduces the effect of fragmentation.

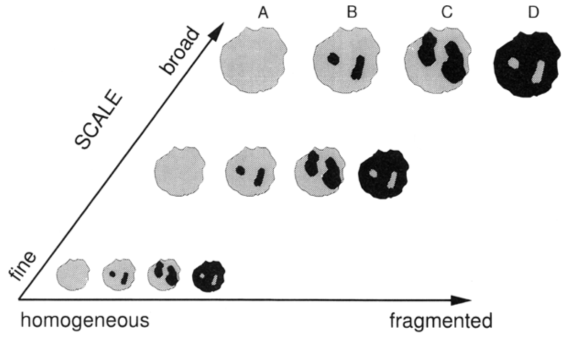


*Figure 4-18.* Pattern and scale from homogeneous to fragmented. Fragmentation occurs at every scale and appears as a continuum. A landscape can be considered fragmented at one scale and homogenous at another (from Wiens 1994, with permission).

Fragmentation dynamics are strongly influenced by human decisions and by land policy. Staus et al. (2002) have found a higher fragmentation rate in private rather than in public forested land in the Klamarth-Siskiyou ecoregion (Pacific US coast) during the period 1972–1992 (see Figure 4.19).

Fragmentation can be increased not simply by reduction of patch size but also by the isolation of patches produced by large roads. Brotons & Herrando (2001) have observed the severe effect of highways on the distribution of birds in an agricultural matrix. In particular, forest birds seem more sensitive to the presence of such barrier. Noise produced by traffic does not seem the only factor impacting bird presence. Probably, other factors like the decrease of connectivity between the forest fragments are also important.

Fragmentation in tropical areas strongly affects the survival of large trees, which are unusually vulnerable. Large trees, as argued by Laurance et al. (2000), are more prone to uprooting and breakage near forest edges where wind turbulence is frequent and higher. Large trees are frequently invaded by lianas (woody vines) that benefit from light and nutrients but which reduce the survival of trees (Figure 4.20). But the higher exposure to sunlight and evaporation also contribute to tree desiccation. The reduction of large trees affects fruit production, flowers and shelter for animal populations.

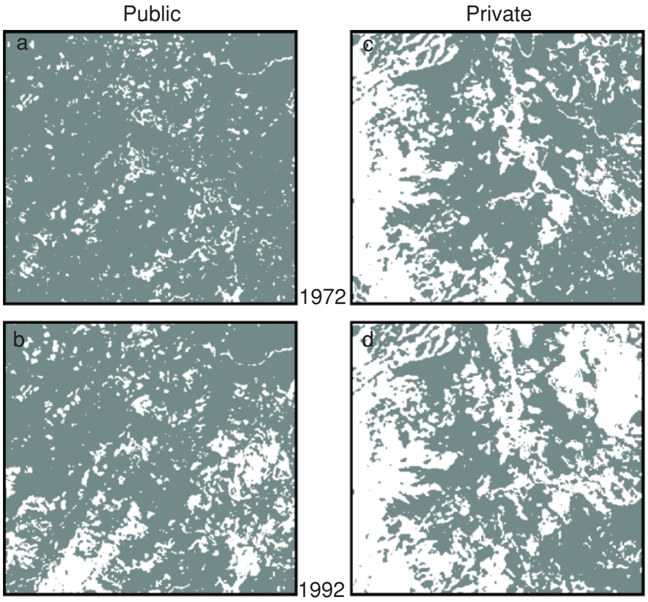


*Figure 4-19*. Different patterns of changes in forest and nonforest land on public and private land in the Klamath-Syskiyou ecoregion, located on the border between Oregon and California (from Staus et al. 2002, with permission).

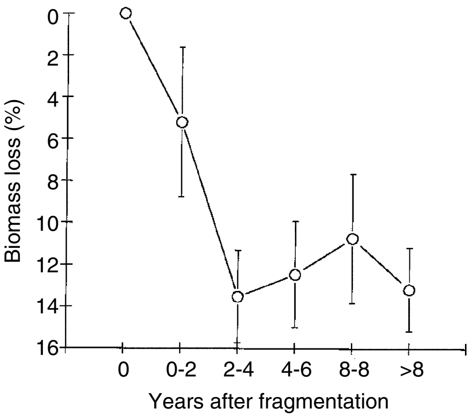


*Figure 4-20*. Biomass collapse in Amazonian forest after fragmentation (biomass loss versus years after fragmentation) (from Laurance et al. 1997, with permission).

## 4.3.2 Scale and patterns of fragmentation

Fragmentation is a scale-dependent process. Fragmented vegetation can have a different spatial arrangement and produce different effects on other ecological processes.

To describe the dispersion of fragments in an area, it is necessary to consider different attributes of the fragments such as density, isolation, size, shape, aggregation and boundary characteristics.

The isolation of patches increases geometrically as the density of the fragments decreases. The fragments become smaller and more influence is received from the surrounding matrix. If fragments are aggregated, their isolation is smaller than in conditions of equi-dispersion.

We have different types of fragmentation. According to Lord & Norton (1990), when an intact area is divided into smaller intact fragments, we have a "geographical fragmentation". This process has received a lot of attention from conservation ecologists for its implications for nature conservation. This pattern can be analogous to a coarse-grained landscape (Table. 4.1).

At the other extreme we can have fragments at the scale of individuals or small plots. It is the case with small remnants of native vegetation embedded in an alien matrix and the fragmentation is considered as "structured fragmentation" and is analogous to "fine-grained landscape. Fine-grained fragmentation generally presents patches close to each other and the contrast between patches and matrix is shallow, creating a pseudocontinuum.

While geographical fragmentation is associated with forest ecosystems, structural fragmentation may be associated with a broad range of conditions.

Fragmentation effects on organisms largely depend on the scale of perception of the focal species. Generalists are less affected by fine-grained fragmentation than specialists.

Fragmentation increases the vulnerability of patches to external disturbances, for instance wind storms or drought, with consequences on the survival of these patches and of the supporting biodiversity (Nilsson & Grelsson 1995).

The scale of fragmentation has a direct impact on organisms. Large fragments maintain a good subset of species but small fragments have only few species, generally the more generalist ones. Thus, specialists disappear from smaller patches when the fragmentation is at a fine-scale. This could be the reason for a sufficient diversity in temperate regions facing a fine-grained fragmentation when compared with the more specialist species of tropical areas.

The patterns of fragmentation are prove to the effects of many natural and manmade variables. The presence of agricultural proximity is a good estimator of fragment probability in the bottomland hardwood forest. But access, urban development, ownership, fencing and regional differences are other secondary parameters useful to predict type and modality of fragmentation (Rudis 1995). For instance, Fuller (2001) has utilized LANDSAT Enhanced Thematic Mapper Plus band 6 to evaluate the forest fragmentation in Loudoun County, Virginia based on the thermal responses of developed areas versus intact woodland.

Fragmentation reduces the size of woodlots but also the habitat quality. Belanger & Grenier (2002) have noted an increase of woodlot density in St. Lawrence Valley (Quebec, Canada) with the increase of agriculture, but the size of woodlots was observed to be decreasing. Fragmentation was found to increase, moving from traditional dairy agriculture to more intense cash crop agriculture (Figure 4.21).

Large fragments have more species, are less disturbed and lower road access than smaller ones. Large fragments are uncommon or rare and their importance is high for nature conservation issues.

Fragmentation depends on human use but the human use is also affected by the fragmentation rate. This is relevant in regions such as the Mediterranean, where several changes in land use occurred across the centuries, modifying the behavior of people according to the new characters of the fragments.

Fragmentation can be observed at any scale, and tree-fall gaps are one important factor increasing heterogeneity and fragmentation. Tree-fall gaps can be considered a distinct habitat in a forest differing in vegetation structure (e.g., foliage density, tree size distribution), plant species composition, resource abundance and microclimate conditions. Birds are particularly sensitive to slight changes of habitat features and probably have the capacity to recognize tree-fall gaps especially as preferred foraging sites. In fact, in tree-fall gaps, resources are particularly abundant and this depends on tree-fall gap size, on the age of the gaps and

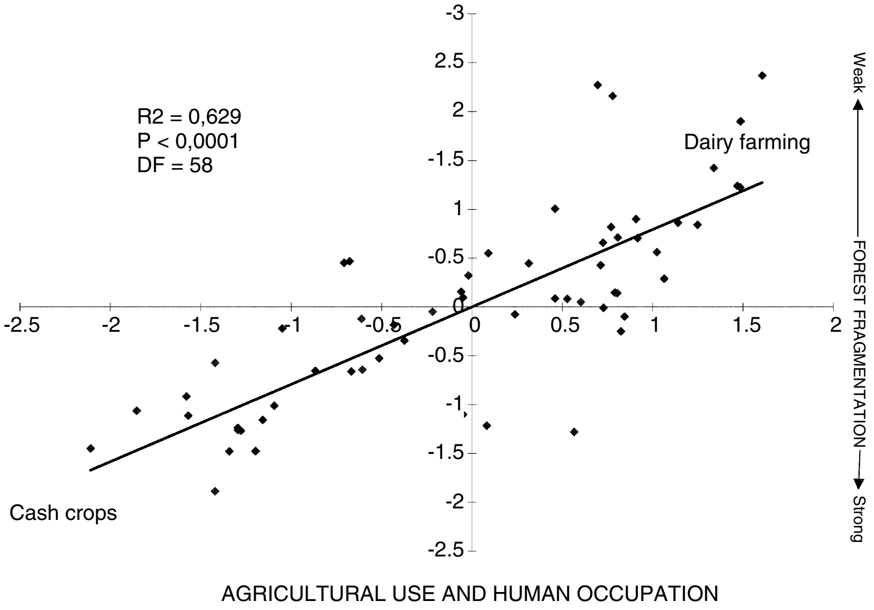


*Figure 4-21*. Relationship observed on the first axis of a canonical correlation between the scores of the first PCA axis that characterizes the agricultural landscape in 59 country municipalities in southern Quebec (Canada) and human population densities, with different forest fragmentation indices. Forest fragmentation increased from dairy farming toward a cash crops (from Belanger & Grenier 2002, with permission).

the surrounding forest tracks. In spring, many migratory birds are attracted by these gaps because food is more abundant here (Blake & Hoppes 1986).

### 4.3.3 Community composition and diversity in fragments

Small woodlots have less species than the biggest ones and there are more generalists in small rather than in larger woodlots. More specialized species increase with the increase of the woodlot area. Blacke & Karr (1987) found more that 66–72% of species are more strongly influenced by habitat variables. Birds breeding in the interior forest and wintering in the tropics are more affected by reduction (fragmentation) of forest habitat (Figure 4.22). The area effect is disputable according to neighboring habitats. In fact, if there are suitable habitats around a woodlot, these habitats could be incorporated by some species, but if the woodlot is separated by agricultural fields, in this case, the habitat constraint is stronger and the isolation is higher, negatively affecting the presence of species.

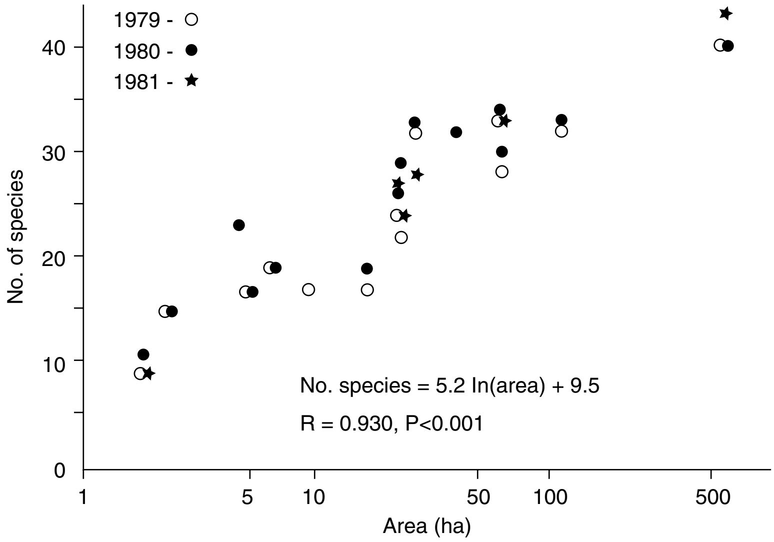


*Figure 4-22*. Number of breeding species plotted as function of natural logarithm of an area of woodlot in east-central Illinois (from Blake & Karr 1987, with permission).

The continuous loss of forests across the USA will probably have negative effects on birds, although actually 3-year studies have demonstrated good stability in populations in woodlots (Blake & Karr 1987), but this does not exclude that in a longer time frame, negative effects could appear and, consequently, monitoring activities are needed to control these trends.

Large patches of nothofagus forest in south-temperate rainforests are more heterogeneous than smaller patches. Bird diversity decreases according to the patch size. This effect is also evident in the cases in which patches are not far from the main forest or from other patches and apparently shrubby corridors occur. For instance, the main causes of the decrease in abundance and diversity of Chilean avifauna depend not only on habitat destruction. But also the clearing of understory may be a negative factor because many species are breeding in the shrub layers or find resources at this height (Willson et al. 1994).

The landscape composition has been found to be important by Rodewald & Yahner (2001) in influencing avian communities in central Pennsylvania. In forests disturbed by silviculture practices, forest-associated, long-distance migrants, forest-canopy and forest-understory-nesting species were found to be more abundant than in forests disturbed by agricultural practices. These authors argue that the type is more important than the extent of the disturbance.

Ground-beetle (*Coleoptera: Carabidae*) diversity has been found to be lower than expected in forest remnants in French agricultural landscapes and quite similar to crop and land edges. This data has been discussed by Fournier and Loreau (2001) in terms of the marginality of the role of small forests in preserving beetle biodiversity. However, other results have been found by Davies et al. (2001), working on the effect of the experimental fragmentation of native eucalyptus of Australia on 325 species of beetles. Fragments seem not to affect colonization and extinction, richness and extinction rates.

When tropical forests are fragmented, an immediate loss of biodiversity is experienced by the stands. Laurance et al. (1997) have found a dramatic loss of above-ground tree biomass in forest fragments in central Amazonia (36% in the first 10 to 17 years after fragmentation) inside 100 m of fragmented edges. Trees experience tree mortality due to microclimatic changes and elevated wind turbulence. The major decline in biomass occurs from 0 to 4 years after fragmentation (Figure 4.23). Despite the temperate fragmented forests, in which the diversity, especially birds, is maintained at relatively high levels and species also move a long distance to colonize a site, in the tropical forests, short distances between fragments and the continuous forest (70–650) represent true barriers for movements of birds. Obligate army ant followers disappear within 2–3 years from isolation. Insectivorous birds are heavily affected by isolation. A fundamental role is played on the isolation by the surrounding vegetation after logging or agricultural use. Woodlot surrounded by Vismia, a dominant vegetation after forest removal by burning and cattle pas-

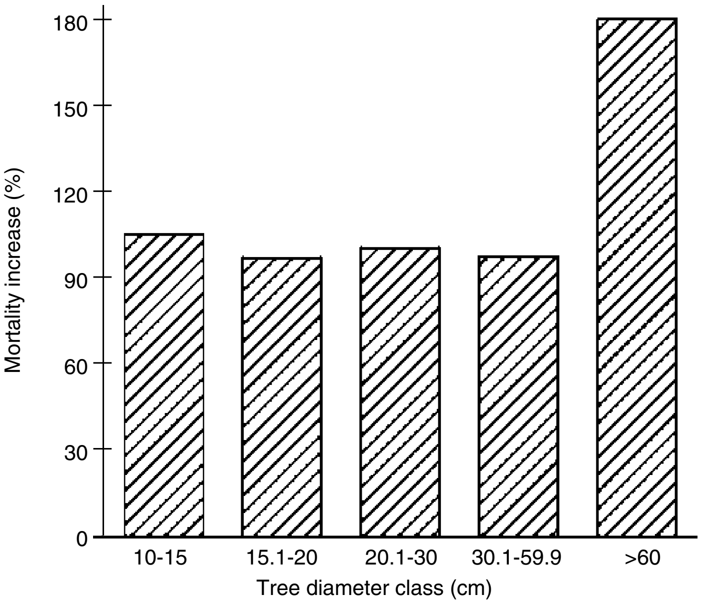


*Figure 4-23.* Increased mortality of tree close to edge in tropical fragmented forest and tree diameter class (from Laurance et al. 2000, with permission).

ture, are considered more isolated by birds than plots surrounded by Cecropia, a vegetation that occurs where forest is removed by logging but not by burning (Stouffer & Bierregaard 1995).

Tropical rainforests cover less than 7% of the planet's land mass but support half to two thirds of the plants and animals on Earth. The sensitivity of tropical forests to fragmentation has been investigated by Bierregaard et al. (1992) during the Biological Dynamics of Forest Fragments Project. Distance effects, fragment size, edge effects, biotic changes were some of the more important issues were considered. Eighty metres of non forest is enough to present a barrier for mammals, insects and understory birds living in a fragment. One, 10 and 100-hectares are the size of fragments at which most of species of insects, mammals and birds are sensitive. After fragmentation, birds moving more across fragments and also the density increases, at least after 200 days after logging. This clearly shows how birds have the capacity to move away from fragments.

The hypothesis that small patches contain subsets of larger organisms was discussed by Cutler (1991) (Figure 4.24) studying mammals in the Great Basin of western North America. Actual mammal composition is the result of the selective, deterministic extinction of species of originally richer fauna. In the Florida keys, the deforestation is producing a decrease in birds. For some sensitive species, the loss of habitat exceeds the actual loss of deciduous forest. This means that habitat requirement for sensitive species is not limited to area size but also to surrounding characters (Bancroft et al. 1995).

Fragmentation in shrub/steppe habitats negatively affects the breeding distribution of shrub-obligate species (Knick & Rotenberry 1995). The difficulties in shrub/steppe restoration may cause irreversible loss of habitat and negative consequences at long-term scales on shrub-obligate species.

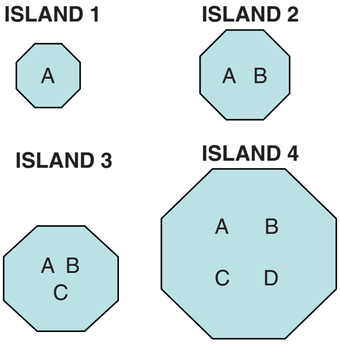


*Figure 4-24.* The species found in fragments are a subset of assemblages of larger plots (modified from Cutler 1991, with permission).

In old-growth montane forests on Vancouver island (Pacific Canada), the effect of fragmentation on bird assemblages was less dramatic than in other areas (Schiek et al. 1994). This probably depends on the fact that old-growth forest evolved within heterogeneous montane forests. It could also depend on the lower contrast between old-growth and logged areas compared with forests and agricultural/urban areas, from which most of fragmentation studied was carried out.

Tscharntke (1992) has found that fragmentation of Phragmites habitats is producing severe effects on insects and birds. An important point stressed by this author concerns the significance of habitat fragmentation that is not limited only to the size of patches but also to the mean shoot diameter. Further, small patches of Phragmites receiving more light have greener leaves than individuals in large, dense patches and some species of aphids are positively correlated with fragmentation.

The fragmentation of midwestern grasslands has pauperized the breeding bird communities (Herkert 1994). Five species (Savannah Sparrow, Henslow's Sparrow, Bobolink, Eastern Meadowlark) have been found to be sensitive to patch size. The increase of farmlands has dramatically reduced the size and distribution of native grasslands. This fact has determined the decline of many birds (Figure 4.25).

Fragmentation of suitable habitat, in this case traditional agricultural land, increases the risk of extinction in Belgian primrose (*Primula vulgaris*) popula-

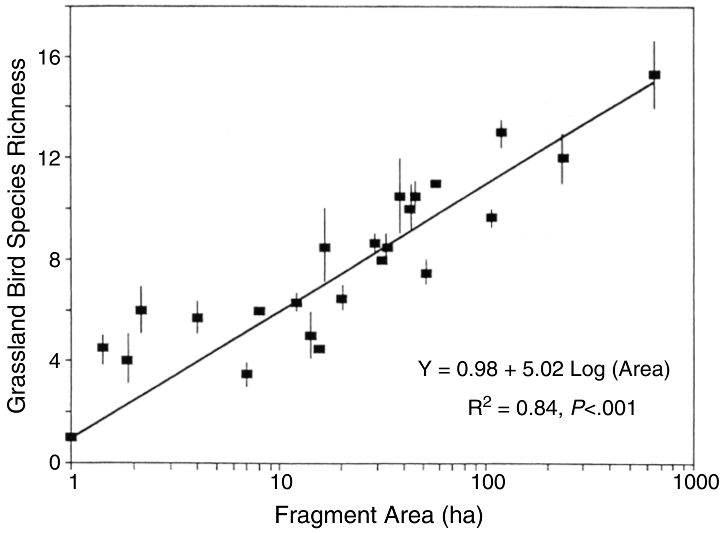


*Figure 4-25.* Bird species richness of grasslands plotted against the area of fragments. Symbols represent number of species found per site in 1987–1989 censuses (from Herkert 1994, with permission).

tions as documented by Endels et al. (2002). They argued that long-term survival of the primrose is at risk if land use practices do not change drastically in the near future.

In boreal European forests, landscape fragmentation has been observed to negatively affect the breeding success of black grouse (*Tetrao tetrix*) and capercaillie (*Tetrao urogallus*) either in terms of forest rarefaction or in terms of destruction of older forests (Kurki et al. 2000).

Mosaic context is a further element that can reduce or mitigate the effects of fragmentation. Bayne & Hobson (2002) have observed that the apparent annual survival of male ovenbirds (*Seiurus aurocapillus*) is lower in small forest fragments (<15 ha) in farmlands (34%) than in forestry fragments (56%) or in continuous forest (62%). These authors aurgued that lower nesting and pairing success observed in small fragments were probably caused by permanent dispersion rather than by fragmentation increasing mortality. At the same time, the age of first-time breeding males was higher in fragments in farmland (59%) than in forestry fragments (47%) and in continuous forest (45%).

Population decline is variable according to the traits of the species considered. Davies et al. (2000) have found that decline appears more in rare species than abundant species, isolated species are more affected by fragmentation than species that are not isolated. The body size does not seem to be correlated with fragmentation effects and that among the species that decline; predators are the group that decline most. Finally, taxonomically-related species respond differently to fragmentation processes.

Fragmentation of riparian flora in rivers is commonly produced by dams. These act as barriers that reduce the capacity of flora to spread along the rivers (Jansson et al. 2000) and the role of river corridors (Figure 4.26).

### 4.3.4 Species, guilds and fragmentation

Some species are sensible to habitat size, these species are called "area-sensitive". Forest-interior breeding species such as oven brirds and Kentucky warblers are in decline due to fragmentation (Gibbs & Faarborg 1990).

The effects of fragmentation of tropical forest on dung and carrion beetle communities was studied by Klein (1989) in the Central Amazon. Fragments had less, rare and dispersed species. This difference was particularly evident when 1 ha fragment was compared with undisturbed forest. The movements of beetles was interrupted by the clear cut, and only after a secondary regrowth were some beetles able to move into fragments, although the distance was a few meters. Probably, the microclimate and especially the desiccation at the border of the woodlot creates prohibitive conditions for the forest-understory beetles.

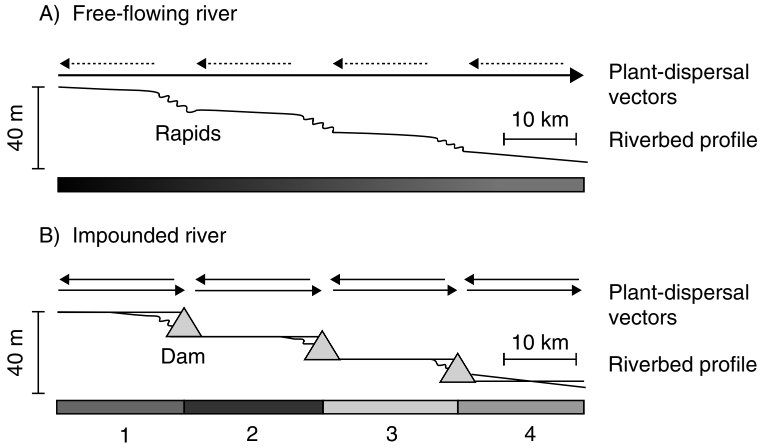


*Figure 4-26.* Flora in impounded rivers is hypothesized to react with local organization and separation (increasing fragmentation) when compared with a free-flowing river (from Jansson et al. 2000, with permission).

The role of dung and carrion beetles as destroyers of nematode larvae and other gastrointestinal parasites of vertebrate is very important in controlling diseases. Increasing the fragmentation of tropical forests and reducing the numbers of such beetles we can expect an increase of diseases in vertebrates.

When the effects of habitat fragmentation are observed at the scale of singular species or groups of related species, it is possible to find interesting surprises and unpredicted results. It is the case of the scorpion *Cercophonius squama* and Amphipods, Family *Tallitridae* as reported by Margules et al. (1994). On a time lag of 8 years, 3 before the fragmentation and 5 after fragmentation in treatment and control plots of Australian hardwood forest dominated by the eucalyptus, the fragmentation had no effect on the abundance of the scorpion. Different results for the amphipods, which decreased markedly after the fragmentation and were more numerous in small than in larger remnants (Figure 4.27).

Probably scorpions, an ancestral animal, using a fossorial behavior during dry periods has the capacity to escape the environmental stress of fragmentation. This is not the case for amphipods, more sensitive to microclimates and with a younger evolutionary history. This is a good example, showing that when we study fragmentation at the level of species, the results may be completely different.

Management should be carried out according to the behavior of populations and landscape scale and subpopulation in the remnants, rather than considering the simple number of species.

*Malacosoma disstria* is a forest tent caterpillar that has outbreaks of different duration according to forest structure (Roland 1993). The amount of forest edge per square km is a good predictor of the duration of outbreaks.

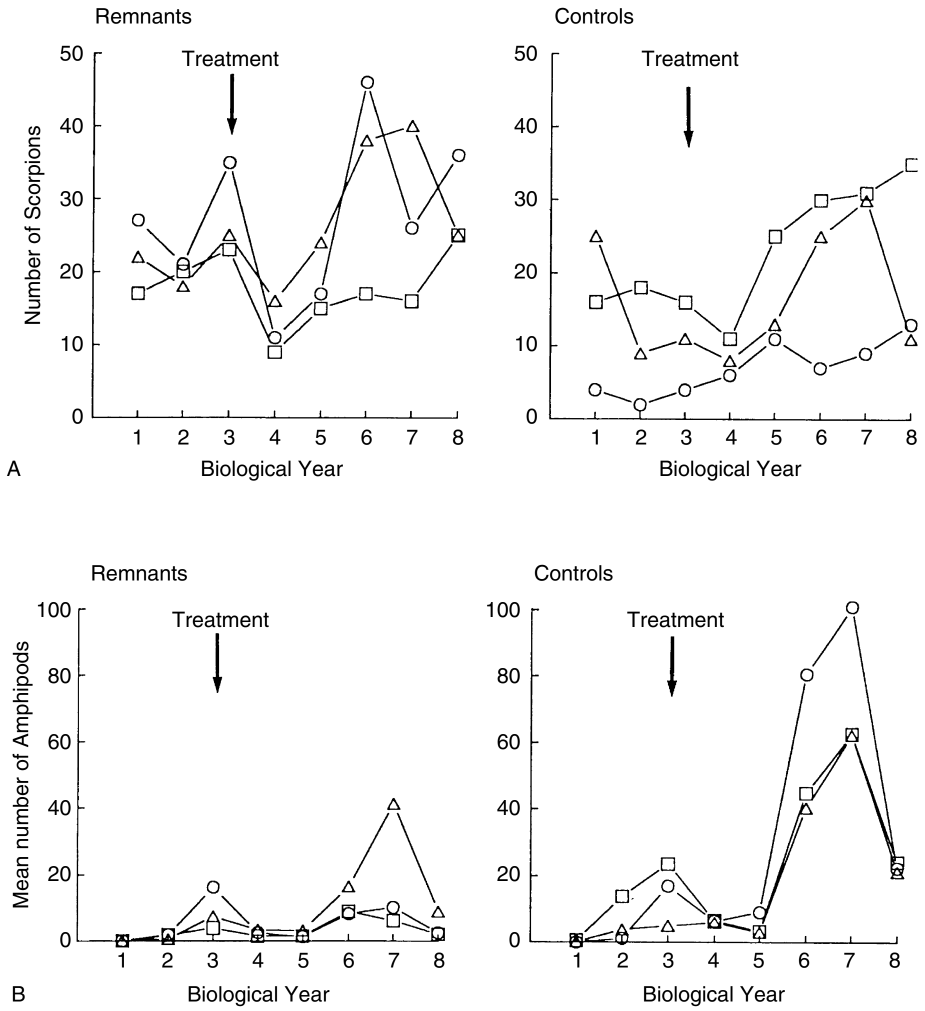


*Figure 4-27.* A: Total numbers of the scorpion *Cercophonius squama* recorded in each forest remnant size for each year ○ small, □ medium, △ large. B: Mean numbers of the amphipod, family Tallitridae, in each forest remnant size for each year ○ small, □ medium, △ large (from Margules et al. 1994, with permission).

Probably, parasitoides are less efficient in controlling *Malacosoma disstria* in the fragments. As other lepidopteran species, *Malacosoma disstria* lay more eggs along the edge and egg predation on this species is apparently at a smaller level than in the forest interior.

Along the edges, the more favorable micro-climatic condition, higher temperatures, reduce the period of larvae development, reducing the risk of predation compared with larvae in continuous stands (Figure 4.28).

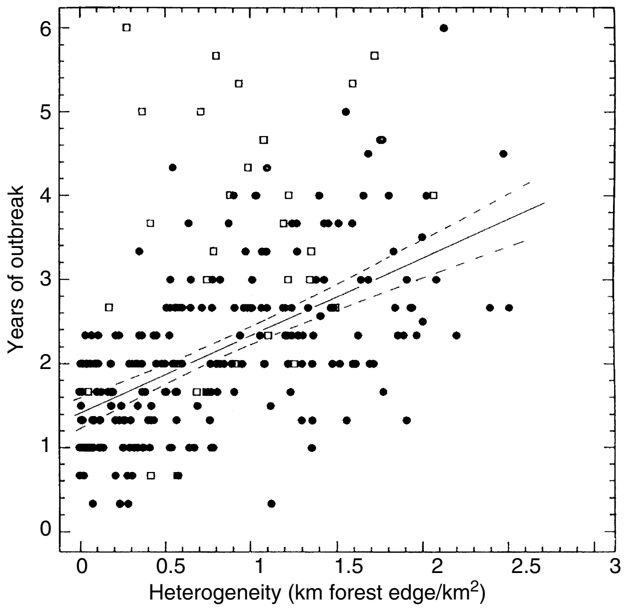


*Figure 4-28.* Mean duration of forest tent caterpillar outbreaks for 261 townships, in relation with forest heterogeneity. (from Roland 1993, with permission).

Species sensitive to habitat fragmentation are less efficient in moving and colonizing new habitats, with a consequently lower dispersal ability (Villard & Taylor 1994). Birds of the African tropical understory forests are particularly sensitive to fragmentation (Newmark 1990). Rare and forest interior species of birds are more adversely affected by habitat reduction. The maintenance of corridors could be a local extinction mitigation action.

Nest success and annual reproductivity are negatively affected by forest fragmentation of the rufous treecreeper (*Climacteris rufa*) in agricultural regions of southwestern Australia, as described by Luck (2003). The effects of fragmentation are also relevant for juvenile survival rates and habitat quality. The combinated effects of different variables under fragmentation stress have been considered the causes of decline of this threatened species.

Insect pollinators in sub-tropical dry forests, in Northern Argentina declined, decreasing the size of fragments but, conversely, honeybees (*Apis mellifera*) increased their frequency of flower visits (Aizen & Feinsinger 1994).

Despite the high rate of alien species in small isolated woodlots, invaders are stopped by light competition, low in interior woodlots and of cropland isolation combined with a low capacity to move with the alien species. The fragments have an edge of dense shrubby vegetation that prevents alien species from entering. But contemporarily, the warmer sides of the edges are more attractive to alien species (Brothers & Spingarn 1992).

In the urban area of Stockholm (Sweden), the Parus guild showed a high probability of occurence only in forest patches larger then 200–400 ha. Dimensions of forested patches, but also large areas of urban open land, industrial settlements and large bodies of water negatively affect the distribution of resident birds, as reported by Mortberg (2001) (Figure 4.29).

## 4.3.5 Habitat fragmentation and extinction

The effect of fragmentation of bird diversity has been documented in the San Antonio upland forests of Colombia by Kattan et al. (1994). In this area, the avian census of 1911 has been compared with data from 1959, 63 and 89-90 years. The loss of 24 species or 31% of the original avifauna is relevant information on the level of fauna impoverishment in these landscapes. These authors, carrying out the more recent census and the comparison, argued that the high rate of extinction is mainly due to the position of many species at the upper limit of their altitudinal distribution and that the more vulnerable assemblages were understory insectivores and large canopy frugivores.

The work of Kattan et al. (1994) is important from many points of view; firstly because the history of bird decline is fully documented and secondly because the effect of fragmentation in large part depends on the biogeography of the species and on the complexity of the foraging structure.

Fragmentation produces changes in organism distribution and relative patterns. In old-growth forests in Sweden, Berglund & Jonsson (2003) have

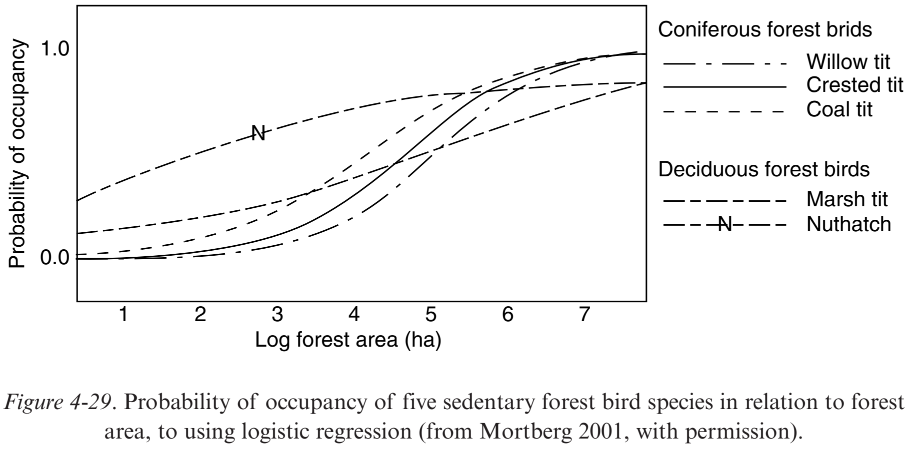


*Figure 4-29*. Probability of occupancy of five sedentary forest bird species in relation to forest area, to using logistic regression (from Mortberg 2001, with permission).

observed a nestedness in species communities of plants and fungi. Nestedness refers to a species-poor site comprising a subset of richer ones. Rare and Red-list species have been found in large patches. But nestedness is also present in small patches if these are of high quality. This result is extremely useful to modulate conservation strategies. From a conservation perspective, such small areas of high quality must be considered.

Changes in metapopulation dynamics have been observed in the bog fritillary butterfly (*Procolossiana eunomia* Esper) in fragmented habitats of Belgium and Finland by Mennechez et al. (2003). Using direct observations and capture-mark-recapture methods in homogeneous and fragmented habitats, these authors suggest that habitat loss and fragmentation affect dispersion more than demography. In homogeneous habitats, demography is lower but stable during a 10-generation period. The dispersal drops dramatically in fragmented areas.

### 4.3.6 Predation and fragmentation

Isolated woodlots generally experience more predation. Recently, Wilcove (1985) has found a higher predation in small than in large woodlots. But predation was higher in suburban neighborhoods than in isolated farmland woodlots. Placing artificial open-cup nests on the ground and at 1–2 m above ground, the predation was higher in both cases than in experimental cavity nests. Considering that most of the neotropical migratory songbirds construct

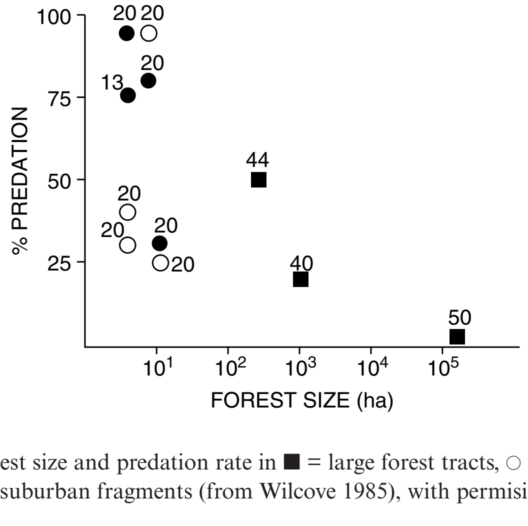


*Figure 4-30.* Forest size and predation rate in ■ = large forest tracts, ○ rural fragments, (●) suburban fragments (from Wilcove 1985), with permision).

open-cup nests, the decline of these species by predation could be more than a consistent suspect (Figure 4.30).

In large forest blocks in Virginia, predation on artificial nests varied from 5 to 40%, according to many vegetation variables and predator community pressure (Leimgruber et al. 1994).

Fragmentation of prairies and marshlands is moving very quickly in some regions of the world such as Canada and the USA, under the impact of a modern industrialized agriculture, producing the decline of sensitive species like the Lesser prairie-chicken (*Tympanuchus pallidicinctus*) that has declined by >90% over the past 100 years, as reported by Fuhlendorf et al. (2002). Although many aquatic birds, such as waterfowls, have resilient capacities to buffer the habitat losses, the vanishing of large natural breeding habitats tremendously increases the risk of predation. Pasitschniak & Messier (1995), using artificial nests placed at different distances, simulated predation risks at the finest edges. The predation risk of a nest of a waterfowl is related to distance from edge in dense nesting cover but no edge effect has been observed in idle pastures or delayed hay fields. This could depend on the abrupt edge between these cultivations and more accessibility by predators. Thus the edges in a man-made landscape could be less important than vegetation structure. The argument has been differently questioned by other authors. Predation of ground nests in prairie fragments in Missouri was studied by Burger et al. (1994). The artificial nests in prairies <15 ha were predated more than in large prairie remnants (37% v 13.9%). Nests placed at a distance < 60 m from woodlands had less probability to be successful then artificial nests placed farther away ( 28.7 v 7.9% predation). Distance from woodland seems to depress predation in ground nests, and the attributes of the surrounding landscape are important to evaluating predatory risk (Bergin et al. 2000).

The fragmentation of holartic forests has altered many dynamics of small herbivores than undisturbed forest. The disappearance of cycles of abundance moving towards the south is mainly due to an increased pressure from predators. Andren et al. (1985) have studied the predator pressure on tetraonids, employing dummy nests.

The predation pressure was higher in the south, as predicted, and the main predators are corvid birds that are more abundant in the southern regions. The abundance of corvids is positively related to the farming system, to the fragmentation of the forest and to a more heavy human disturbance regime (Figure 4.31).

A different narrative emerges when a seagrass landscape is considered. This landscape is naturally fragmented and this habitat offers refuge to juvenile blue crabs, although crab survival varies temporally and survival increases with habitat complexity, regardless the size of seagrass fragments (Hovel & Lipcius 2001).

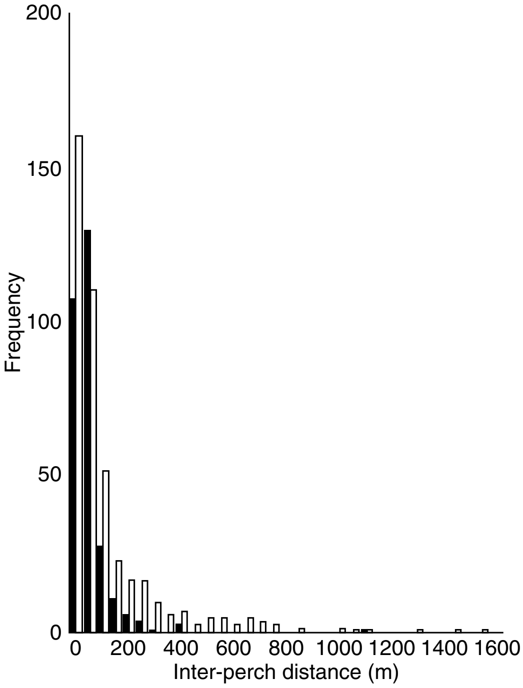


*Figure 4-31.* Frequency distributions of distances moved by tawny owl (*Strix aluco*) in Monks Wood (shaded) and the farmland (open) (from Redpath 1995a, with permission).

### 4.3.7 Island size and isolation: A key to understanding fragmentation

We consider extremely important to verify the effect of area and isolation in a true island landscape in order to understanding the fragmentation process better.

The investigation of Martin et al. (1995) in Gwaii Haanas Archipelago of British Columbia on birds breeding on islands of sizes from 1 to >100, 000 ha, has demonstrated that many factors have to be considered when the fragmentation process is investigated.

The analysis of the landscape pattern seems extremely important. Four major factors were recognized to be responsible for differences in habitat structure among the islands. First, on small islands, more edges increase the shrub cover and the proportion of edge is consequently higher on small than on larger islands. Second, small islands are more exposed to wind storms, tree cover is more sparse and more undergrowth is present. Third, the less isolated islands receive more rain than the isolated ones and the moss biomass is consistently smaller. Fourth, on larger islands, the black-tailed deer, *Odocoileus hemionus* is more abundant than on smaller islands. In some cases, the smallest islands have no possibilities to support permanent deer populations. The browsing effect of deer is very strong on understory vegetation.

The effect of area on bird species is important only on small islands. On decreasing the island size, some species became rare but others became more common, further decreasing the island size. A correlation was found between habitat features and birds. Only for a small proportion of species did island size and isolation appear important. The area per se appeared not enough to explain bird species diversity and abundance in Gwaii Haanas Archipelago but habitat features, although in some degree related to island size and isolation, are important factors.

### 4.3.8 Habitat fragmentation and animal behavior

Habitat fragmentation modifies some aspects of animal behaviour such as movements and food searching. The response of small mammals to fragmentation was tested by Diffendorfer et al. (1995) in three 0.5 ha plots with larger patches 5000 $m^2$, medium patches 288 $m^2$ and small patches 32$m^2$ from 1984 to 1992 on cotton rats (*Sigmodon hispidus*), deer mice (*Peromyscus maniculatis*) and prairie voles (*Microtus ochrogaster*).

As expected, the animals moved a larger distance and a lower proportion of animals moved, increasing the fragmentation. But no source-sink mechanisms have been verified, as also indirectly suggested by Menzel et al. (1999) in their conclusions after an investigation on the effects of a wildlife opening procedure in western North Carolina. Control of the demographic status seems important to validate such methodologies.

The tawny owl (*Strix aluco*), a common nocturnal predator in Europe, seems sensitive to woodland fragmentation. The foraging behavior of 24 owls radio-tracked by Redpath (1995a,b) were analyzed in continuous woodland and farmland with sparse woodlots. In fragmented woodlots, owls had a longer interperch distance and perch times. Males have longer perch times compared to females. And males in fragmented woodland spend 40% more time in flight then males in continuous woodland. Fragmentation greatly influences owl activity and behavior (Figure 4.32).

In some species, adaptation to fragmentation can be innate. It is the case for the desert-dwelling mountain sheep (*Ovis canadensis*). This species is adapted to living in steep, mountainous, open terrain, which is naturally fragmented, evolving a high vagility among fragmented habitats in condition where suitable corridors can persist (Bleich et al. 1990).

Dispersion reduces the isolation effect but this encourages the spread of diseases and increases the mortality of moving organisms (Burkey 1995).

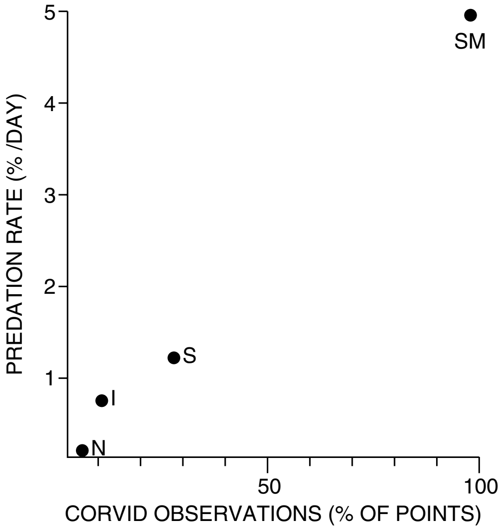


*Figure 4-32.* Relationship between predation rate and the number of corvid observations. N- the northern area, I- the intermediate, S- the southern area in southernmost Sweden used by Goransson and Loman (1976) quoted by Andren et al. 1985, with permission.

## 4.3.9 Measuring the effects of fragmentation

Hinsley et al. (1995) have employed many variables to characterize fragmentation in relation to birds (Table 4.3): Area and structure, isolation, connectedness, surrounding land use. The turnover of species was calculated according to Diamond (1969) as: (E+C)/(S1+S2)x100%, where E and C are the number of species extinctions and colonizations respectively. S1 and S2 are the number of breeding species present in the two years. The turnover rate of birds was higher in small rather than large woodlots, although some census biases could obscure the results.

The turnover was found in the relationship with plot area. However, higher turnover in small woodlots was due to the changes of common species.

With increasing dimensions of woodlots the turnover was present especially in rare species such as the great spotted woodpecker while common species were excluded by stochastic extinction.

Gu et al. (2002) have applied a model of metapopulation coupled to the history of a changing landscape to evaluate the effects of fragmentation on four threathened polyporous fungi (*Amylocystis lapponica*, *Fomitopsis rosea*, *Phlebia centrifuga*, and *Cystostereum murraii*) in eastern Finlandia, simulating a static and a dynamic landscape. The species have demonstrated sensitivity to

*Table 4-3*. Variables, describing woodland area and structure, isolation, connectedness and surrounding land use, used in the stepwise multiple regression analyses (from Hinsley et al. 1995, with permission).

| *Area and structure* |
|---|
| Woodland area, ha |
| Perimeter, m |
| Shape |
| Density of canopy layer |
| Density of shrub layer |
| Density of field layer |
| Number of habitats |
| *Isolation* |
| Area of woodland within 0.5 km, ha |
| Area of woodland within 1.0 km, ha |
| Length of hedgerow within 0.5 km, km |
| Length of hedgerow within 1.0 km, km |
| Distance to nearest wood, km |
| Distance to nearest wood of ≥ 2ha, km |
| Distance to nearest village/town, km |
| *Connectedness* |
| Number of hedges connected to wood |
| Number of ditches connected to wood |
| Number of dirt roads to/from wood |
| Total number of linear connections |
| *Surrounding land use* |
| % of perimeter adjoined by cereal |
| % of perimeter adjoined by rape and beans |
| % of perimeter adjoined by root crops |
| % of perimeter adjoined by other crops |
| % of perimeter adjoined by grass |
| % of perimeter adjoined by non-crop usage |

the structure and dynamics of the landscape when applying the dynamic model. Only *A. lapponica* has demonstrated sensisitivity to the static model.

Most of the effects of fragmentation have been evaluated in terms of change in the demographic patterns of species. Recently, however, the effect of fragmented habitats has been considered in terms of modification of secondary characters of species and more specifically in Fluctuating Asymmetry (AF). Fluctuating Asymmetry is a pattern of bilateral variation that is normally distributed around a mean of zero in morphological traits, where symmetry is the normal state. The appearance of asymmetry is linked to environmental instability (van Valen 1997) and is used as an indicator of environmental quality but also of genetic variation in populations or in individual quality (David et al. 1999; Palmer & Strobeck 2003; Oleksyk et al. 2004). For instance, leaf asymmetry of the holm oak (*Quercus ilex*) from SE Spain has been found to increase with the increase of stress dependence (Hodar 2002).

Fluctuating Asymmetry has been found to increase in populations of bank vole (*Clethrionomys glareolus*) under the constraint of landscape fragmentation in the Mon-Saint-Michel Bay, by Marchand et al. 2003).

The asymmetry in the tarsus length have been utilized as an indicator of stressors on birds living in rain forest remnants of Kenya with different sizes (Lens et al. 2002). Indirect evidence of the effects of habitat fragmentation has been argued by Schmidt & Jensen (2003) as a change in mammalian body length. During the last 175 years, the body length of Danish mammals has changed at the lowest rate in medium-sized species, but increased in smaller and larger species. Small mammals have increased, but larger mammals have decreased in body length. The authors do not exclude other selective forces, such as traffic, but the hypothesis of a cause-effect between fragmentation and body length sounds very attractive and worthy of further investigation.

### 4.3.10 The complexity and unpredictability of fragmented landscapes

In a fragmented landscape, the complexity of the patterns and of the relative processes may be so extreme as to confound the results of the investigation, as argued by Arnaud (2003) studying the metapopulation genetic structure and migration pathways in land snails (*Helix aspersa*). Some species, such as the mistletoe, which are patchily distributed, have reactions to fragmentation that are directly correlated to the size of the remnants. This species is dispersed by birds that deposit the digested seeds. It is noted by Norton et al. (1995) that the distribution of this species is linked to birds that eat fruits and disperse the seeds, and the corridors between *Eucalyptus salmonophloia* are apparently not used enough by disperser birds, because no mistletoe plants have been found. It is possible to conclude that fragmentation in different places has different effects.

## 4.4 CONNECTIVITY, CONNECTEDNESS AND CORRIDORS

### 4.4.1 Introduction

Landscapes are heterogeneous across a broad range of scales. The heterogeneity as discussed in the chapter 5.2 is characterized by the presence of patches with different isolations from patches of the same type. It is obvious that isolation creates problems for the diffusion of organisms and reduces the survival capacity when the organisms are small in number. Three important concepts can address the problem of patch isolation: Connectedness, Connectivity and Corridors.

Connectedness, or proximity, is the degree of physical distance between patches. It is a structural (descriptive) attribute of a landscape mosaic and can be mapped (Baudry 1984) (Figure 4.33). Thus, the matrix is the most connected element of a landscape. Generally, we refer connectedness to other elements of landscape as woodlots, hedgerows, river beds, etc. The opposite situation is called isolation and specific metrics have recently been provided by Tischendorf et al. (2003).

In some rural areas, the hedgerow network is the most connected component after the field matrix. For instance, woodland connectedness (potentially) plays a fundamental role for species that needs tree cover for their movements. For instance, the increase of woodland connectedness after land abandonment has favored the diffusion of the wild boar in most of the mountain landscapes of Europe.

It is intuitive that road and traffic represent factors reducing connectivity especially for small and medium-sized animals like hedgehogs (*Erinaceus europaeus*). Huijser & Bergers (2000) have calculated that road and traffic reduce hedgehog density in two provinces of the Netherlands by 35%.

Merriam (1984) utilized the term connectivity as a "parameter to measure the processes by which the sub-populations of a landscape are interconnected in a demographic functional unit". Connectivity can be used as the inverse correlate of hostility of interpatch habitat. In general, connectivity measures the amount of favorable habitat available to a focal species. For instance, distance between favourable patches and size of habitat patches are sufficent to

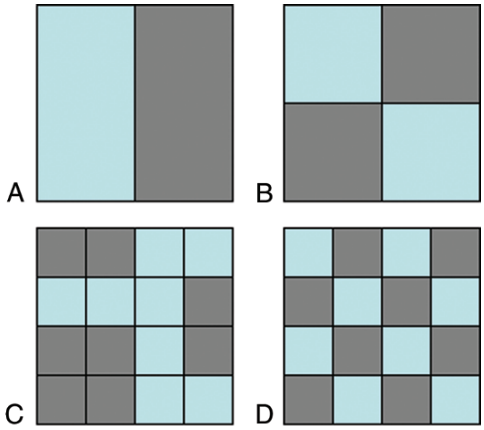


*Figure 4-33.* Example of four mosaics with the same percentage of two land covers but spatially arranged according to different values of decreasing connectedeness (A to D).

predict the distribution of the mountain vizcacha (*Lagidium viscacia*) (Walker et al. 2003).

Often, the term connectivity is utilized not for focal species but only as a potential factor that improves the circulation of "generic" species. The importance of connectivity is stressed by Sondgerath & Schroder (2002), who employed spatially explicit modeling.

A recent revision of papers dealing with connectivity Goodwin (2003) discusses the open problems with this conceptualization. Specifically, Goodwin noted the asymmetry between papers dealing with connectivity as an independent variable and a dependent variable. Studies on connectivity as a dependent variables are very few. At the same time, studies on structural are more frequent than studies on functional connectivity. The author suggests that future reasearch on landscape connectivity should focus on:

"(1) elucidating the relationship between landscape structure, organism movement behavior, and landscape connectivity. (2) Determining the relationship between different measures of connectivity, particularly structural and functional measures, and (3) empirically testing model predictions regarding landscape connectivity".

Landscapes with high potential connectivity can assure more survival probability to isolated populations, as confirmed by Merriam (1984) in the Canadian rural landscape for some species of rodents.

In some cases, the connectedness is low but connectivity is high; here, we can assume that a functional corridor exists.

In landscapes in which natural covers have been severely fragmented "connectivity" for focal species can be increased if traditional farming is maintained by economic incentives, as stressed by Baudry et al. (2003), and this fact ispires optimism for intensively cultivated areas on which management improvements are rarely applied (Figure 4.34).

Connectivity has been successful investigated by Bunn et al. (2000), applying the graph theory in the Coastal Plain of North Carolina for two focal species, American mink (*Mustela vison*) and the prothonotary warbler (*Protonotaria citrea*).

See also Jordan et al. (2003) for an example of application of the graph theory to the study of patch connectivity of a metapopulation of *Pholidoptera transsylvanica* (*Orthoptera*) (Figure 4.35).

### 4.4.2 Corridors: Structure and functions

Corridors are functional structures in a landscape and their presence is fundamental to mitigate the effect of fragmentation or *vice versa* to increase the penetration of alien species. In other cases, corridors are structurally recogniz-

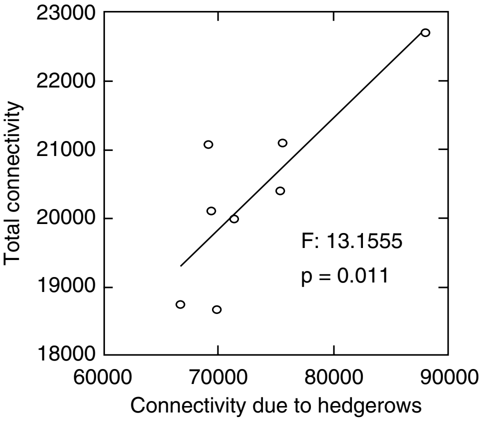


*Figure 4-34.* Relationship between total connectivity and edge connectivity according to a simulation in different types of rural landscape (from Baudry et al. 2003, with permission).

able like hedgereows. The corridor concept is not clear and is often used with different meanings. The controversy on the exact role of corridors in a landscape is open and largely depends on the different context in which corridors are considered (Simberloff et al. 1992; Collinge 2000), although the corridor paradigm is extensively used in master planning and land remediation (Pirnat 2000). In organic farming, the utilization of corridors of natural vegetation has also been successfully tested (Nicholls et al. 2001).

Corridors can be defined as narrow strips of habitat surrounded by habitat of other types. Across a corridor, plants and animals can move more easily, but a great variability in species behaviour exists along corridors.

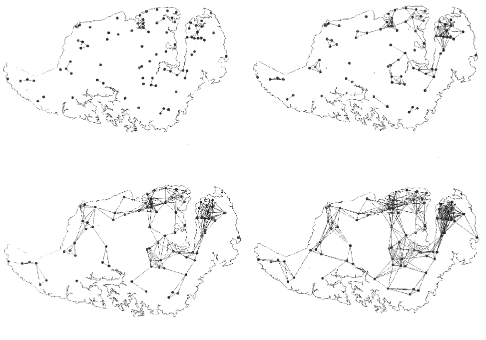


*Figure 4-35.* Graph edges with increasing threshold distance from 5, 10, 15 and 20 km. The focal species threshold (max distance between favorable habitats) reconsiders the four potential scenarios (from Bunn et al. 2000, with permission).

For some species of micro-mammals, corridors are difficult to verify (Mabry & Barrett 2002).

In fact, there is little evidence that animals use structured corridors like hedgerows and fencerows, although differences have been observed according the sexes. For instance Danielson & Hubbard (2000), in an experimental mosaic have trapped more males of *Peromyscus polionotus* than females in isolated patches. The same is true for many plants that need to disperse, germinate and grow in soil conditions that cannot be assured by a narrow belt of vegetation (the corridor) (see, for instance, Tikka et al. 2001).

Corridors can be created by topography such as a pass along the mountain ridge crossed by migratory birds, or by hydrological cycles such as a river bed, or by human tropical or boreal forest clearance.

Rivers are the most important and extensively studied corridors (Ward et al. 2002). Recently, Planty-Tabacchi et al. (1996) have found a great number of alien species moving along river corridors. This has been explained as a direct effect of the intermediate disturbance regime and of the physical structure of the riparian corridors. The patchy structure of the riparian landscape, due to the combination of seasonal flooding, temporary ponds and in general extreme environmental conditions from dry to permanently by submerged habitat, allows the presence of indigenous and alien species. The invasibility of the river depends on the various hydrological and geomorphological zones along it. The apparent effects of dominance of alien species on native plants are mitigated by the high landscape temporal heterogeneity of the system, due to a seasonal disturbance regime.

In experiments on fragmentation conducted on a moss matrix, Gilbert et al. (1998) have found that the maintenance of corridors between the isolated patches reduces the rate of loss of species richness and that the patterns of gamma diversity, the diversity of the entire fragmented system, is higher when the fragmentation is mitigated by the presence of corridors (Figure 4.36).

Corridors seem to be vital for the maintenance of large home-range mammals such as the cougar (*Felix concolor*). This species travels on average 5.5 miles per night and thus needs a lot of corridors to maintain its living standard. Telemetry seems to be a very promising approach to understanding the mechanisms of landscape corridor selection by highly-vagile animals, then putting this information on a map and processing the data in a GIS, appears a very promising technique, although administrative and political restrictions in planning space for cougars and other large carnivores are the real limiting factor of the preserving action (Beier 1993).

Recently, using satellite telemetry techniques, Morreale et al. (1996) have tracked the oceanic movements of 8 female leatherback turtles (*Dermochelis coriacea*) after egg laying on the Costa Rica beaches (Figure 4.37). Apparently, all the individuals maintained a narrow route between the breeding

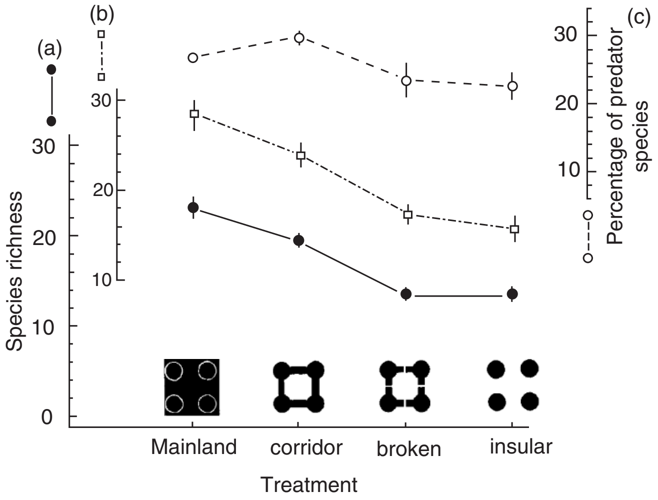


*Figure 4-36.* Species richness of moss animal community according to the different experimental manipulation of moss cover (mainland, corridor, broken, insular). (a) local species diversity; (b) gamma diversity, (c) richness of predators (from Gilbert et al. 1998, with permission).

beach and the open ocean. The existence of a marine corridor is presented and discussed. In fact it is not casual that different exemplars in different years were following the same oceanic route. A gap in these results depends on the uncertainty for the factors determining the corridors. Probably, these corridors are created by food distribution and the rarity of this turtle could be a signal for reducing oceanic productivity. Mobile corridors have been observed in marine landscapes at seagrass/sand ecotones by Brooks & Bell (2001). Drift algae (*Hypnea cervicornis*) has been observed to be more colonized by epifaunal amphipod assemblages (*Ampithoe longimana* and *Cymadusa compta* represent 77% of the total abundance) when such algae are drifting between seagrass/sand ecotones, as a consequence of experimental defaunation of drift alage. Clumps of algae that were moving through the seagrass/sand ecotone had more amphipods than clumps that did not move and were stationary.

The width of corridors is expected to be an important attribute of these structures. There is some evidence from an experiment conducted on *Microtus aeconomus* (Pallas) by Andreassen et al. (1996) that this species has more dispersing capacities when intermediate corridors 0.4 m-wide are provided (Figure 4.38).

The value of corridors and their practical use in conservation are strongly affected by the quality of land cover that surrounds the areas occupied by the metapopulations. This is outlined by Ferreras (2001) in studies conducted to the Iberian lynx (*Lynx pardinus*) (the most endangered species of all the

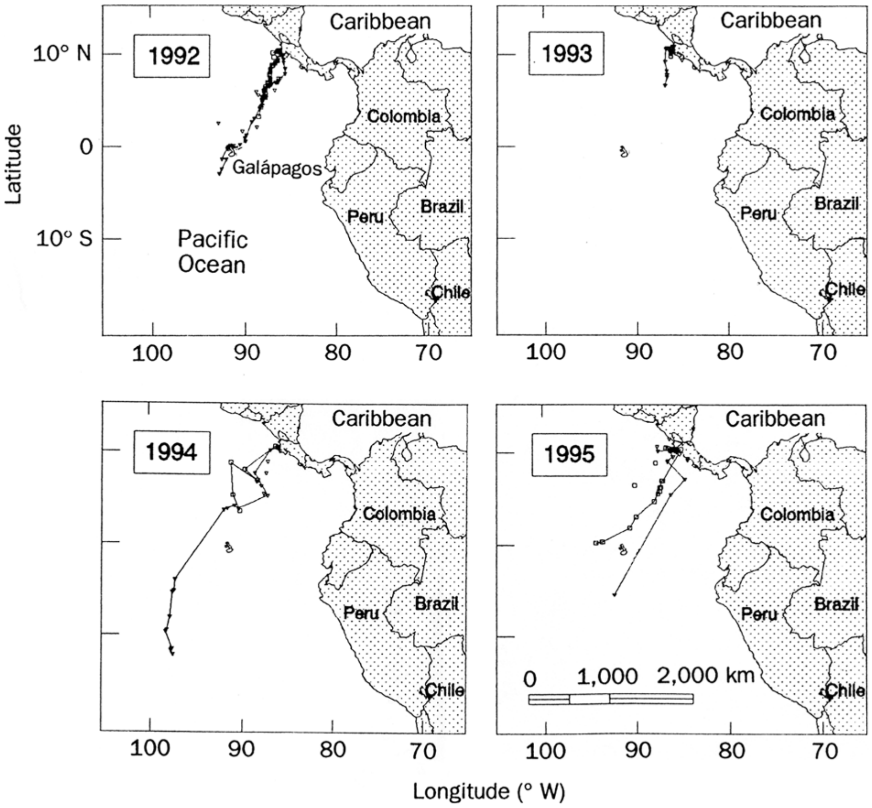


*Figure 4-37.* Migration routes of leatherback turtles monitored by satellite radio tracking from the Costa Rica breeding beaches to the deep ocean, after egg deposition (from Morreale et al. 1996, with permission).

Felidae) in the Doñana region. The dispersal of this species is strategic for conserving genetic variability and also for demographic recruitment, but dispersion is strongly affected by the presence of wide open areas that reduce the possibility for lynx to move outside the home range of isolated populations. The improvement of land cover quality inside the home range and into the surrounding matrix seems the only practical measure to adopt in that region. This study indicates the difficulty of any intervention in the land mosaic when it is not possible to recreate suitable habitat for the endangered species. Often, large-sized organisms require more environmental attributes that we can perceive from our investigations. Finally, the investigation of life traits of which the performance are strategic to avoid local or regional extinction, seems a solution that must be assured to understand the eco-fields.

*Figure 4-38.* Sibillini Mountains, central Italy. A remnant beech forest creates a belt along the mountain assuring a potential corridor for the animals. The recent expansion of the central Italian populations of wolf (*Canis lupus*) toward the north has probably been facilitated by such types of corridor.

## 4.5 SOIL LANDSCAPE AND MOVEMENT OF WATER AND NUTRIENTS ACROSS LANDSCAPE

### 4.5.1 Introduction

The surface of the Earth shows variability at the landscape scale (1–10 km) and this variability has a strong influence on the large-scale circulation of the atmosphere (Pielke & Avissar 1990; Klaassen & Claussen 1995). For instance, the contrast between a bare soil and a forest soil can create strong breezes. Surface temperature and precipitation are strongly conditioned by the vegetation cover. Bare soil receives four times less precipitation in North America and ground surface is 15° to 25° warmer than in wet soils. The landscape characteristics affect the regional atmosphere and have a strong influence on the global climate. The landscape effect depends mostly on the vegetation height and distribution. Heat and gase exchanges are sensitive to the roughness of the landscape and the exchange between the landscape and the atmosphere is not simply the sum of the exchanges between the different landscape elements.

The dispersion of organisms in a landscape has been assumed to be random and then unpredictable and it has been assumed that distance from the source is the main factor. In reality, the roughness of the landscape due to its

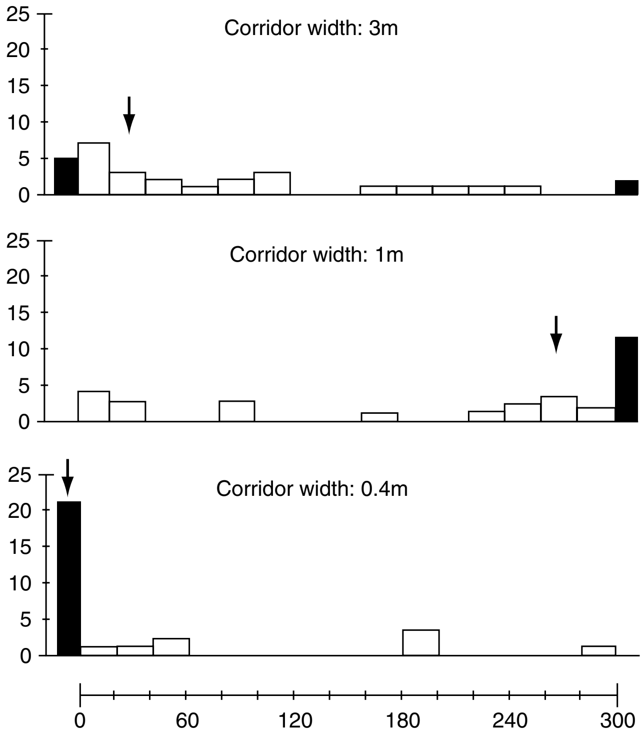


*Figure 4-39.* Frequency distribution of the maximum distance reached from the release point by males of *Microtus aeconomus* (Palls). The black bars indicates the frequency of males that have never left the release patch or have reached the opposite patch (from Adreassen et al. 1996, with permission).

topographic character and vegetation cover create patterns that can be modeled and then predicted. For instance, the effect of circulation patterns of VA (Vesicular-arbuscular) mycorrhizal fungi affect the distribution and functioning of plant communities, altering the succession rate and competition of the plants (Allen et al. 1989). The deposition of propagules by wind is not in relation to the distance in fact, it is not decreasing or increasing the distance, but more linked to complex dynamics that can be understood if the direction and intensity of the wind are known. We have to understand the physical character of a site but also the scale at which an organism reacts with the environment in which selection pressure operates (Figure 4.41).

The recent use of new, more sophisticated sensors, like ground-penetrating radar (GPR) and electromagnetic induction (EMI) (Stroh et al. 2001) has allowed us to distinguish soil discontinuity and to open new approaches to explain the role of edaphic heterogeneity in regulating woody plant distribution.

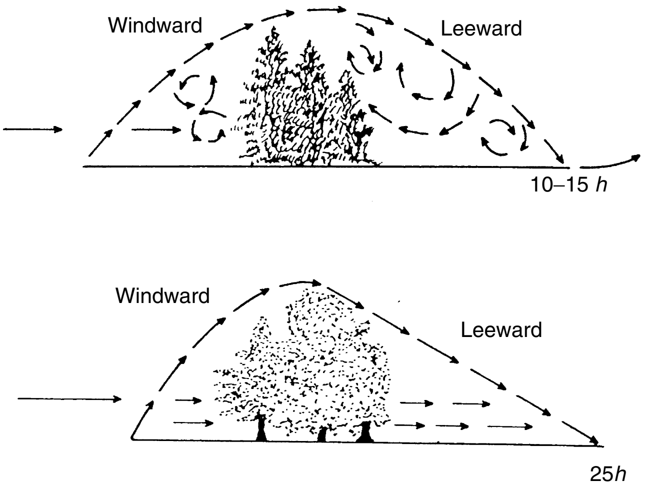


*Figure 4-40*. Effect of windbreak on wind turbulence. Height, porosity and distance of windbreak influence the wind behavior (from van Eimern et al. 1964, with permission).

## 4.5.2 Soil landscape

Soil landscapes play a fundamental role in vegetation patterning. This has been clearly demonstrated by McAuliffee (1994), on studying the landscape evolution, soil formation and vegetation distribution in the Sonoran desert bajadas (Arizona).

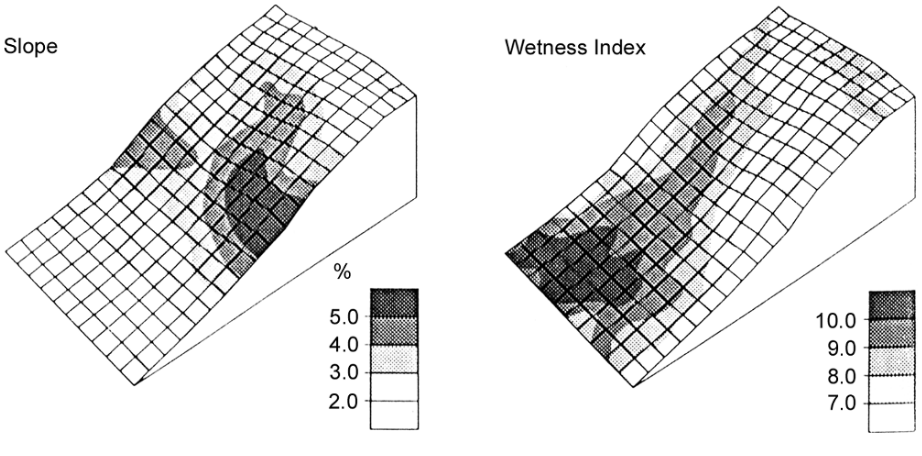
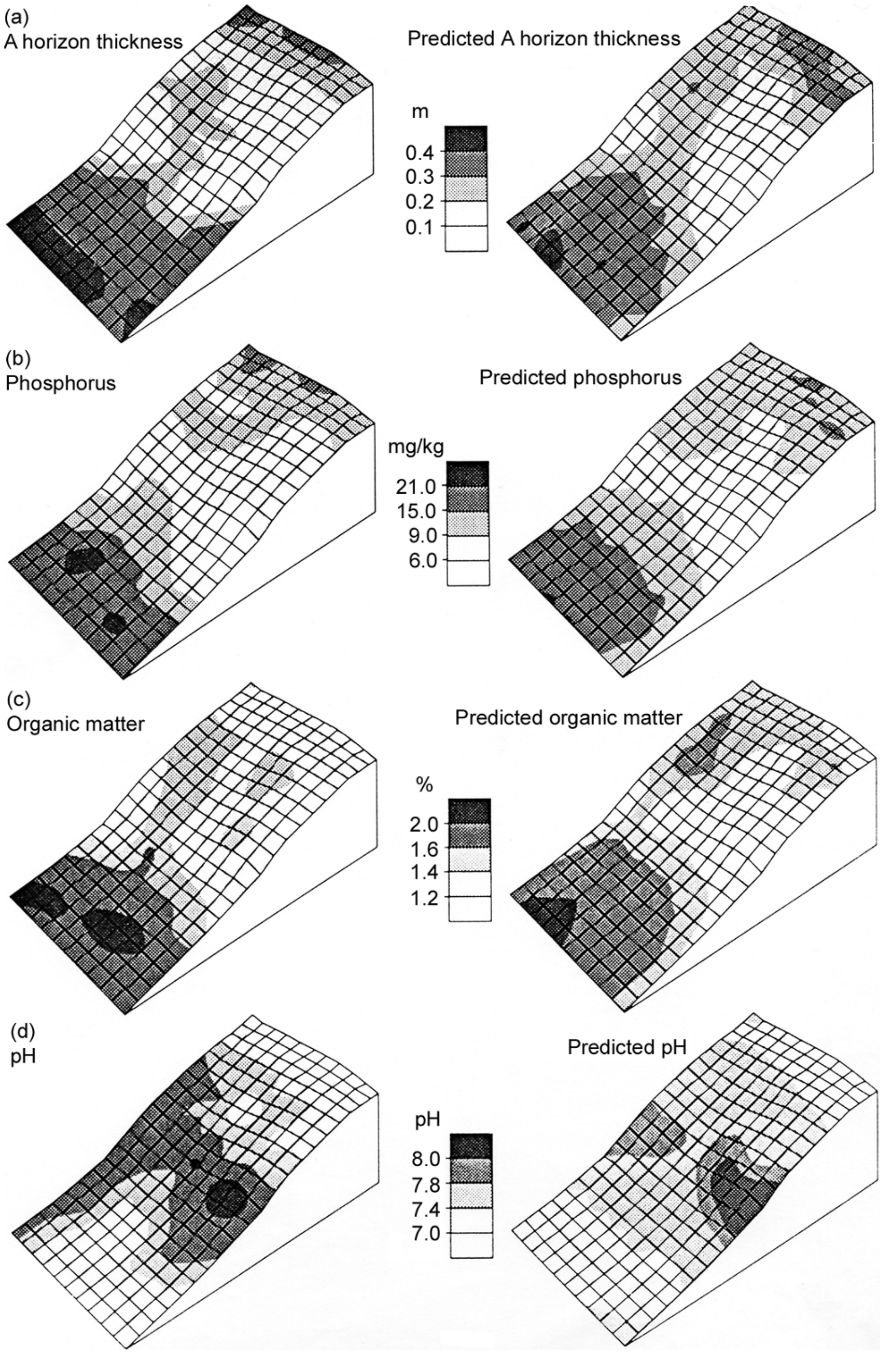


*Figure 4-41*. Slope, Wetness index, A Horizon, P, Organic matter, pH Measured and predicted using a 15.24 m grid-based digital elevation model of the Sterling, CO, site (from Moore et al. 1993, with permission).

*Figure 4-41—cont'd*


(a)
A horizon thickness
Predicted A horizon thickness
m
0.4
0.3
0.2
0.1
(b)
Phosphorus
Predicted phosphorus
mg/kg
21.0
15.0
9.0
6.0
(c)
Organic matter
Predicted organic matter
%
2.0
1.6
1.4
1.2
(d)
pH
Predicted pH
pH
8.0
7.8
7.4
7.0

The Sonoran Desert close to Tucson is a complex mosaic of distinct geological landforms, created by aggradation and erosion of soil at different times. In this area, the soil mosaic has a strong gradient of age and profile development.

Vegetation patterns and geomorphic processes are strongly correlated. A fundamental role has been found in controlling the vegetation pattern by the weathering intrusive versus weathering-resistant, extrusive rocks. Landform age and stability have a strong effect on vegetation. For instance, *Larrea tridentata* occupies many parts of this landscape thanks to a clone-like growth that excludes other species. But in young alluvial deposits, in highly erodable hillslopes and in extremely thin soils that experience severe drought via petrocalcic horizons (caliche), *L. tridentata* suffers from episodes of mortality. In the more drought-exposed parts of this landscape, succulent plant communities can be found. In conclusion, in this landscape, origin, soil formation, plant physiological, demographic and interspecific interactions contribute to create a complex mosaic and allow enlargement of the spatial scale, a relevant framework for studying arid systems. This example can be exported into other regions.

The soil landscape system, as conceptualized by Huggett (1975, 1995) is characterized by a dispersive process of all the debris of weathering (particles, colloids and solutes) influenced by surface and phreatic surface forms. The movements of elements tend to be perpendicular to land-surface forms, altering the topography which, in turn, influences their movement, creating a feedback between the two systems (mobile debris and topography).

It is reasonable to attribute a strong influence for landscape patterns on soil formation (see, for instance, Wang et al. 2002). The topography role can be appreciated using many descriptors but elevation, slope, gradient, slope curvature and slope length, slope direction, contour curvature and catchment area seem most important.

By studying toposequences it appears that minor variations in topography also produce changes in soil properties and dynamics (Heimsath et al. 1997).

Moore et al. (1993), studying a toposequence in a Colorado agroecosystem, have found a good correlation between slope and wetness index with soil attributes (organic matter content, pH, extractable P and silt and sand contents, in A horizon thickness, accounting for about 50 percent of the variability.

Precipitations and their interactions with the landscape depend not only on slope character and soil composition but also on soil cover and use. Figure 4.39 represents the partition of precipitation according to the different land covers, describing the rate of surface runoff, seepage, evaporation and dissolved matter-flow (Ripl 1995) (Figure 4.42).

Soil moisture influences many processes in soil landscape, such as plant productivity, nitrogen and carbon mineralization, and vegetation and animal distribution and abundance. Today, remote sensing procedures, coupled with geostatistic analysis, allow us to estimate the amount of soil humidity on a

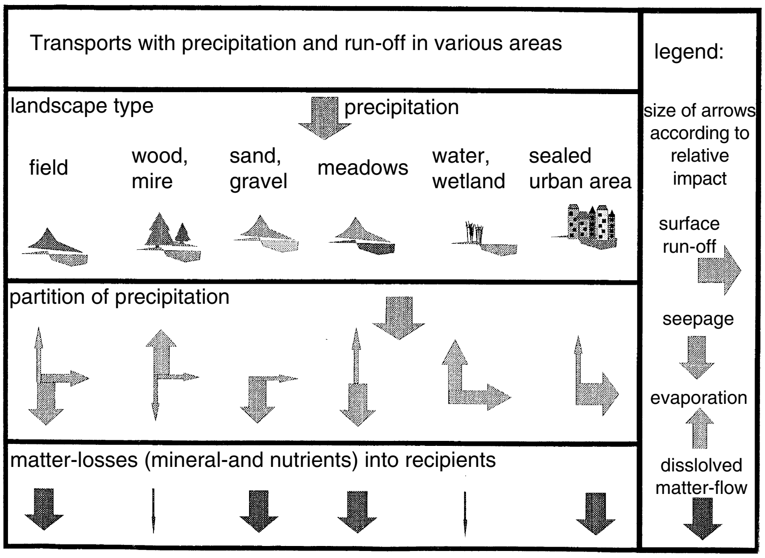


*Figure 4-42*. Description of precipitation and matter losses repartitioned across different components of a landscape (from Ripl 1995, with permission).

monthly basis at a resolution of a 1 km grid (see, for instance, Gimona & Birnie 2002).

In alpine tundra of the Colorado Front Range (Rocky mts., USA), Litaor et al. (2002), applying geostatistical modeling and a fractal approach, have found that large-scale variation in soil composition is correlated to topographics/snow gradients. But at the small and micro-scale, the soil is influenced by the combined effects of cryoturbation, biological activity, parent-material and eolian deposition.

The landscape position plays a fundamental role for instance on the sedimentary chemistry of abandoned-channel wetlands (Swarz et al. 1996). The riparian landscape is a high dynamic system and the soil properties are expected to be influenced by this dynamism. The chemistry of riparian wetlands is influenced by the rate of connectivity with the active river channel. In fact, organic matter and nitrogen are in lesser quantities in sites more connected and sensitive to exportation during flooding events. However, the neighboring agricultural mosaic also has a strong influence on the soil chemistry of the riparian deposits, especially on nitrogen and phosphorous. The time since abandonment is an important control factor. In fact, after the abandonment, the system moves from an open dynamic system to a closed system, in which the circulation of water and materials creates different conditions *in situ*. The organic matter increases and soil develops but the nitrogen content does not seem to increase significantly with time and the content found in old, abandoned deposits is not significantly greater than that found in channels of intermediate age.

Nutrients such as phosphorus and nitrogen are captured and processed differently according the different patch type in a mosaic landscape (Risser 1989, Mander et al. 2000; Kuusemets & Mander 2002). Several landscape metrics explain the nitrogen yeld of streams (Jones et al. 2001) (Table 4.4). This largely depends on the topographic position of vegetation patches and on edaphic conditions. Nutrients move from one landscape unit to another according to the position of each unit. The comprehension of this process is essential to modeling and managing ecosystems. Phosphorous movement is strongly

*Table 4-4*. Metrics used to evaluate the potential loading of nutrients and sediments to streams and to evaluate the "health" of watersheds (from Jones et al. 2001, with permission).

| *Metric* | *Explanation* |
|---|---|
| Riparian agriculture | Percentage of watershed with agricultural land cover adjacent to stream edge. One pixel (30 × 30 m)wide. |
| Riparian forest | Percentage of watershed with forest land cover adjacent to stream edge. One pixel wide. |
| Forest fragmentation | Forest fragmentation index for watershed. Of all pairs of adjacent pixels in the watershed that contain at least one forest pixel, the percentage for which the other pixel is not forest |
| Road density | Road density for watershed expressed as an average number of kilometers of roads per square kilometer of watershed |
| Forest land cover | Percentage of watershed with forest land cover |
| Agricultural land cover | Percentage of watershed with agricultural land cover (pasture/crops) |
| Agricultural land cover on steep slopes | Percentage of watershed with agriculture occurring on on slopes greater than 3 percent |
| Nitrate depostion | Estimated average annual wet deposition of nitrates (kg/hax100) |
| Potential soil loss | Proportion of watershed with the potential for soil losses greater than 2240 kg/ha/yr |
| Roads near streams | Proportion of total stream length having roads within 30m |
| Slope gradient | Average % slope gradient for watershed |
| Slope gradient range | Percentage slope gradient range (maximum minus minimum) for watershed |
| Slope gradient variance | Percentage slope gradient variance for watershed |
| Urban land cover | Percentage of watershed with urban land cover |
| Wetland land cover | Percentage of watershed with wetland cover |
| Barren land cover | Percentage of watershed with barren land cover This includes quarry areas, coal mines, and transitional areas, such as clear cut areas |

linked to particle transportation; then any soil particle accumulation process is an indicator of phosphorous trapping capacity.

The soil quality plays a fundamental role in nutrient retention and dynamics.

According to topography nutrients like C, N and P, they show different concentrations long a soil catena. Schimel et al. (1985) have found an increase of C, N, and P downslope in a short-grass steppe (Colorado). The soil properties are different moving from top to bottom in the rounded hills of the studied area (see Figure 4.43 and Table 4.5). On the summit horizon, the concentration of these three nutrients shows a decrease moving from the top downslope. The backslope is hilly portion in which C,N and P concentration has the minimum concentration. The N availability increases downslope, while the relative N mineralization decreases.

Another relevant factor affecting the cycle of nutrients is linked to the dominant land use of a watershed. The nutrient discharge changes according to the different land uses. Table 4.6 reports the quantities in kg ha$^{-1}$ of different watersheds (Correll et al. 1992). Nitrogen and phosphorous are mostly discharged by croplands.

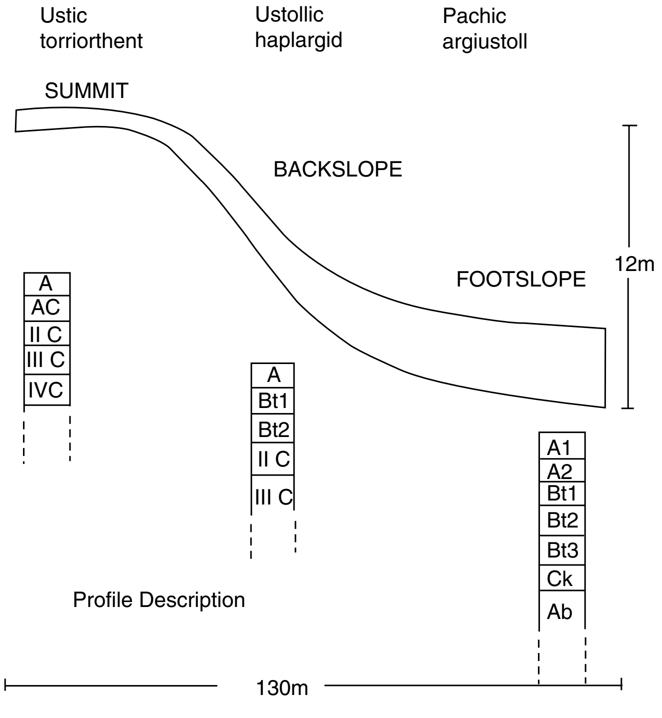


*Figure 4-43.* (a) Different soil horizon along a toposequence in a short-grass steppe catena and (b) the concentration of C, N and P organic in mg/kg (from Schimel et al. 1985, with permission).

*Table 4-5*. Organic C, N and P concentrations in catena soil surface horizons (from Schimel et al. 1985, with permission)

| | | *Concentration (mg/kg)* | | |
|---|---|---|---|---|
| Slope Orientation | Horizon | $C_{organic}$ | $N_{organic}$ | $P_{organic}$ |
| Summit | A | 6900±800 | 921±97 | 124±25 |
| Backslope | A | 5700±400 | 665±92 | 65±16 |
| Footslope | Ai | 209400±1500 | 1937±275 | 206±61 |

Nitrogen availability is the major driver of biomass production. The availability of N is quite high across the planet and this produces a biomass recruitment that in some cases can be considered harmful. This is the case of the ecotones between forest-grassland ecotone in Canada studied by Kochy & Wilson (2004). These authors have found that available soil N (ammonium and nitrate) was higher in burned than in unburned areas, when the areas were not grazed by large ungulates. In the areas intensively grazed, the differences between burned and unburned sites were small.

At the ecotone, aspen invade grassland and this apparently is facilitated by the presence of N when grasslands are not grazed. Fire seems unable to maintain grassland *per se* without grazing. This fact has great importance for management policies when the grassland biome is considered for conservation.

### 4.5.3 The role of riparian vegetation in nutrient dynamics

Peterjohn & Correll (1984) and Correll et al. (1992) have studied the effect of coastal land use and terrestrial community mosaics on nutrient transport to coastal waters. The riparian, deciduous, hardwood forest bordering fields removes over 80% of nitrate and total phosphorous in overland floods and about 85% of nitrates in shallow groundwater drainage from cropland. But the nutrient discharge from croplands is higher than the discharge from pastures

*Table 4-6*. Annual discharge of nutrients on three different watersheds dominated by different land cover. The nutrients are in kg/ha (from Correll et al. 1992, with permission)

| *Parameter* | *Cropland* | *Pasture* | *Forest* |
|---|---|---|---|
| Total-nitrogen | 13.8 | 5.95 | 2.74 |
| Dissolved ammonium | 0.45 | 0.51 | 0.15 |
| Nitrate | 6.35 | 3.20 | 0.36 |
| Total-phosphorus | 4.16 | 0.68 | 0.63 |
| Orthophosphate | 1.20 | 0.32 | 0.15 |
| Atomic ratio of total-nitrogen/total-phosphorus | 1.50 | 3.95 | 1.96 |

and other forests. Estuarine tidal marshes capture organic material and release dissolved nutrients (Figure 4.44).

Different zones of bed structure and stability in a channel control the pattern of bed load transport at the fine scale. But over medium and long periods, the medium bed load yield has a low variability. Local bed load transport is influenced by the local conditions of the channel. The spatial pattern of flow competence and bed load transport is more complex than would be expected from a simple relationship with shear stress (Powell & Ashworth 1995).

The riparian forest has an important role in regulating the upstream-downstream movement of matter and energy. Considering that geomorphic

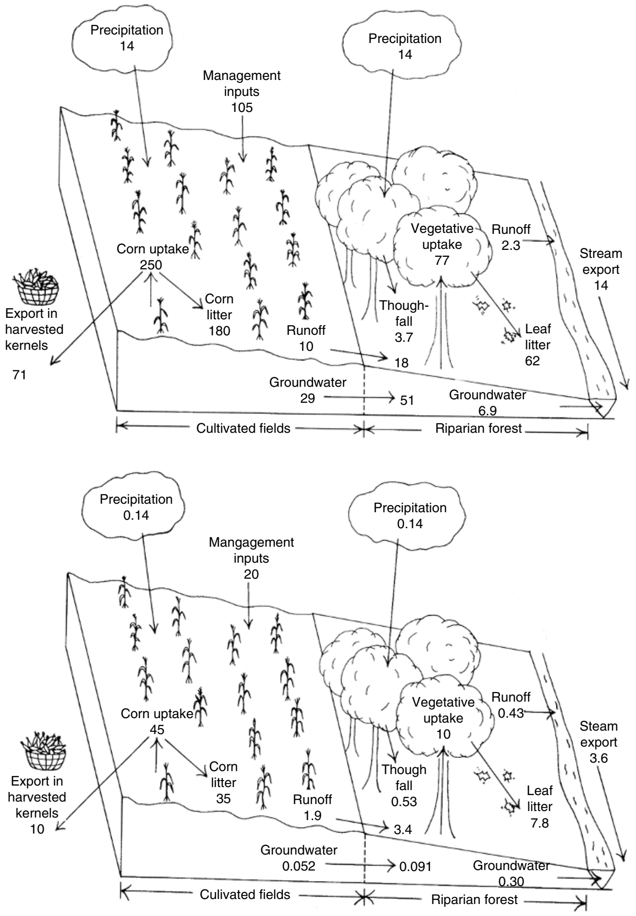


*Figure 4-44.* Diagram of total-N and total-P flux and cycle in the period March 1981 to March 1982 in a small watershed, Rhode River drainage basin, Maryland (from Peterjohn & Correll 1984, with permission).

processes determine the structures of the channels and floodplain and their influence on the capacity of soil to retain nutrients and organic carbon. Two erosional types (E-type characterized by sand deposition and D-type characterized by silt and clay deposits) have a different behaviour in nutrient retention. C, N and P are correlated with erosion/sedimentation processes. D-type riparian forest soil behaves as a sink during flood periods. E-type riparian forests function as a sources, releasing large amounts of C, N and P (Pinay et al. 1992). This demonstrates that a riparian forest does not function as a homogeneous buffer but according to different geomorphic processes, the same forest type can have a different capacity for the retention of nutrients concurrent with the heterogeneity of the patch mosaic.

Kesner & Meentmeyer (1989) have found in the Little River Watershed, Georgia, USA, a massive flow of N especially from anthropogenic sources, but the total balance of N indicates that a buffering process, mainly due to riparian vegetation, occurs despite a large agriculture input. And, once again, the importance of riparian forest is confirmed with strong implications for cropland management.

## 4.5.4 Origin, composition and flux of dissolved organic carbon in a small watershed

Dissolved organic carbon (DOC) has been studied in different locations in the Hubbard Brook Valley by McDowell & Lickens (1988) (Figure 4.45).

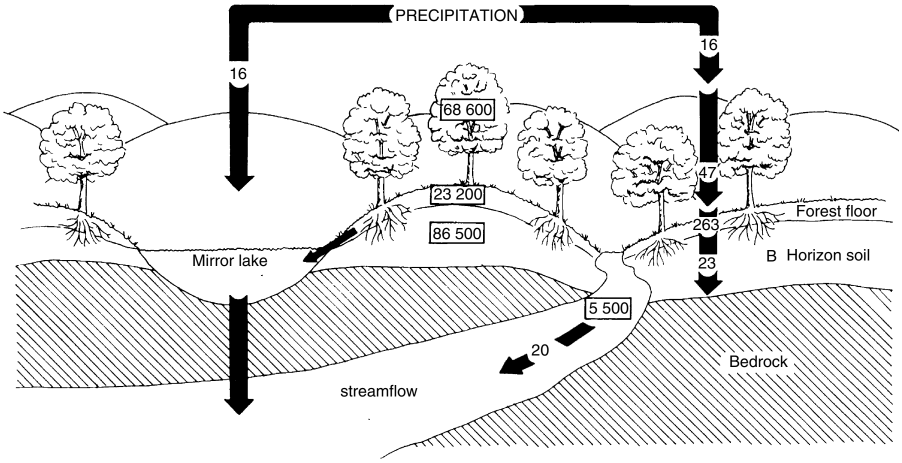


*Figure 4-45.* Movements and standing stock of organic carbon and flux of dissolved organic carbon (DOC) in the Bear Brook Watershed (from MacDowell & Lickens 1988, with permission).

Of special interest from a landscape point of view seems the question posed by these authors “Are there significant changes in the composition of DOC as it moves through the landscape?”

The water flowing across the Hubbard Brook landscape shows an increased DOC with passage through the upper soil horizons. Due to a leaching process, the water is enriched by DOC whilst moving through the canopies and then the forest floor. DOC remains constant, moving from the forest floor to streams and then into the Mirror Lake. DOC decreases on passing through the mineral soil, but carbohydrates increase in sites of high primary production, especially in throughfall and lake water, where the photosynthesis is very high.

### 4.5.5 Leaf litter movements in the landscape

In deciduous forests, the leaf litter represents an important source of nutrients, their movement across different patches mainly depends on topography. The redistribution of leaves influences the heterogeneity of a landscape.

The behavior of litter fall depends greatly on the orientation of slopes and on tree species. Boerner & Kooser (1989) found that net downslope litter movements was larger then vertical litterfall. The Quercus litter was 1.3–1.5 times more redistributed than non-*Quercus* litter and most of the redistribution occurred during January-April leafless season. A different behavior was observed for different slopes and orientation. This in general contributes to maintaining the fertility patchiness in the landscape.

### 4.5.6 Spatial patterns of soil nutrients

Nutrients are present in the soil with a heterogeneous distribution and this pattern is especially evident in the pre and desert regions where the nutrients are scarce. In the previous century, most of the deserts of south-west United States have changed their main land cover from grasses to shrubs. The causes of this dramatic change, largely due to overgrazing, appear different and not very clear. But once a shrub is grown in one location in a short time an “island of fertility” is created (Schlesinger et al. 1995).

Nutrients, like N, in a perennial grassland (*Beteloua eriopoda*) show variation of 35–76% at distances <20 cm, the remaining variance was expressed over a distance of 7 m. In adjacent shrubland in which *Larrea tridentata* has substituted grasses, N variation from 1.0 to 3.0 meters is reached and seems more concentrated under the shrub canopy. This accumulation has also been found for soil $PO_4$, Cl, $SO_4$ and K. In the inter-shrub space Rb, Na, Li, Ca, Mg and Sr are more concentrated. In conclusion, grasslands showing a more fine-grained distribution of soil properties and shrublands have a more coarse-grained distribution of these components. The soil properties could be utilized in semi-desert regions as an index of desertification from grassland across shrublands.

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## Chapter 5

# EMERGING PATTERNS IN THE LANDSCAPE

## 5.1 INTRODUCTION

Landscapes are complex systems that show many different patterns according to the scale of resolution and the component towards which the investigation is directed. Two main patterns are described in this chapter, the heterogeneity and the ecotones. Both are produced by different processes of which disturbance and fragmentation, in particular, are very influential.

Heterogeneity is the main pattern of every landscape and strictly linked with this pattern we find the edges or ecotones. Every pattern produced by processes is in turn a producer of new processes. In particular, heterogeneity has a dramatic influence on many processes across the landscape.

Ecotones are special areas in which different types of habitats meet and where ecological processes are strongly influenced by the co-occurrences of different land attributes. Their role is fundamental to understanding landscape complexity and its functioning.

## 5.2 LANDSCAPE HETEROGENEITY

### 5.2.1 Introduction

Most of the ecosystem-oriented studies have introduced a basal bias by extrapolating the ecosystem from the real world, considering convenience only for homogeneous and quite simple systems.

Recently, environmental heterogeneity has captured the attention of many scientists, with an incredible production of new data at all scaled levels from individuals to landscapes (Pickett & White 1985; Turner 1987; Shorrock & Swingland 1990; Kolasa & Pickett 1991). Most of the actual landscape ecology is oriented towards the study of phenomena interconnected or conditioned by spatial heterogeneity.

Heterogeneity is an inherent character of the land mosaic. This pattern exists at any scale of resolution and can be considered as the structural substrate on which the biological diversity can develop more easily.

Heterogeneity may be defined as the uneven, non-random distribution of objects (Forman 1995) and the analysis of this pattern is of fundamental importance to understanding most of the ecological processes and the functioning of complex systems such as landscapes.

Heterogeneity and diversity are two related concepts in landscape ecology, but while diversity describes the different qualities of the patches, heterogeneity represents the spatial complexity of the mosaic.

Ultimately, three different types of heterogeneity have to be considered:

Spatial heterogeneity. This heterogeneity may be see as a static or a dynamic pattern, namely observed as oriented or ecological entity perspectives (Kolasa & Rollo 1991) (Figure 5.1). Spatial heterogeneity, consequently, effects many ecological processes like soil formation, weathering, plant distribution, animal distribution, abundance and movements, water and nutrient fluxes, energy storing and recycling, etc.

Spatial heterogeneity may be further distinguished into horizontal and vertical components. Horizontal heterogeneity represents the unven distribution of land cover that may be created by human disturbance regimes. For instance, in the Mediterranean basin, most of the landscapes have been shaped by a pluri-millenary human disturbance regime by which the heterogeneity is enhanced by different types of cultivation. Vertical heterogeneity represents the uneven distribution of vegetation above ground, and is more connected with natural landscapes.

Temporal heterogeneity has a similar meaning to spatial heterogeneity but is measured as the variation from one point in the space at different times. Two locations may have an identical temporal pattern but be asynchronous in time, expressing here a temporal heterogeneity.

Functional heterogeneity represents the heterogeneity of ecological entities (distribution of individuals, populations, species, communities). This heterogeneity may appear linked to the life history of organisms at several scales.

Heterogeneity can be observed in the soil composition as focused on by Becher (1995) in which pH, $C_{org}$, $C_{carb}$, texture, saturated hydraulic conductivity, bulk density, pore size distribution soil properties, vary strongly across plots. This variation can be found at all spatial scales from landscape to hundreds to tens meters. This variability can also be found in the vertical soil profile.

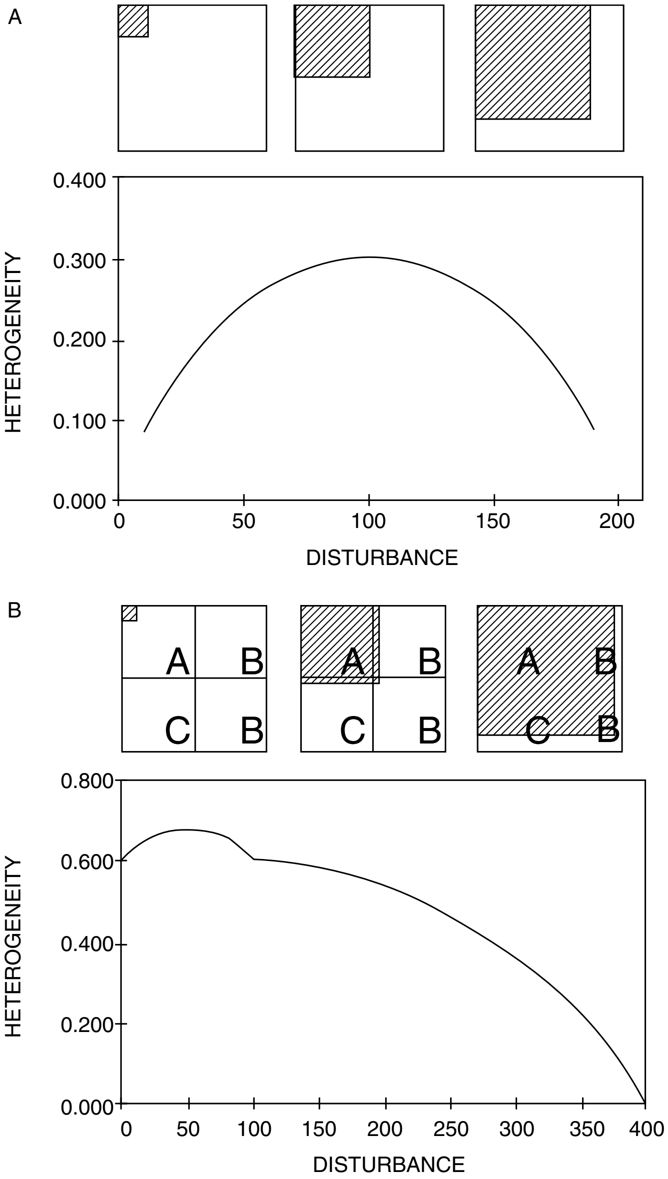

*Figure 5-1.* Habitat heterogeneity as a function of the spatial scale of disturbance. A) diffusion of disturbance in a homogeneous habitat, B) in heterogeneous habitat (from Kolasa & Rollo 1991, with permission).

The effect of geological heterogeneity creates a highly unpredictable system and for this reason a probabilistic approach is used by Hantush & Marino (1995) to evaluate aquifer behavior.

Heterogeneity creates borders, edges and a contrast between different patches. This pattern again originates new processes, influencing, for example, movements of organisms, fluxes of material and energy (Pickett & Cadenasso 1995). Plant and animal assemblages can react in a very short time to any change in mosaic heterogeneity and this can be easily detected by field and/or remote sensing investigations.

Heterogeneity is also a sign of patchiness of the land. The level of heterogeneity can negatively affect some processes. For instance, when open spaces such as prairies are too small, some species of birds, such as skylarks, avoid them, although the character of these open spaces in terms of vegetation and resource availability are apparently very close to sites of larger size.

Heterogeneity, in consequence, plays a very pre-eminent role especially when the interacting scale of the organisms is coarse (Kie et al. 2002).

Heterogeneity may be initiated or exaggerated by way of biological interactions with the environment. Local uniqueness determined by local characters and by past site-related history or distinctiveness is a relevant contributor to spatial heterogeneity.

In the Mediterranean region, heterogeneity in general is positively correlated with biodiversity. In particular, birds and leptidoptera have been found by Atauri & de Lucio (2001) to be strongly affected by heterogeneity (Figure 5.2).

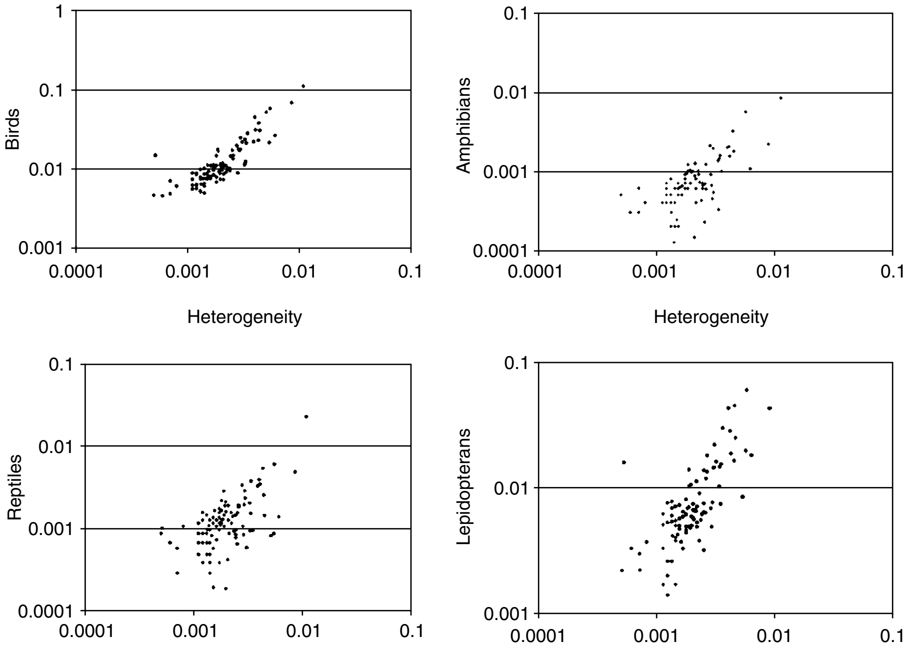

*Figure 5-2*. Relationship between landscape heterogeneity (expressed as landcover type/hectare) and selected groups of animals (from Atauri & de Lucio 2001, with permission).

Dispersal is another relevant factor contributing to spatial and temporal heterogeneity (Levin 1976). Heterogeneity can admit multiple stable states as a polyclimax that can be considered to be a state of spatial variations in the local equilibrium. Heterogeneity is not only conditioned by external factors such as variation in weather, climate and edaphic factors, but also by internal random events such as outbreaks, colonization, etc. At this level, disturbance can be a relevant factor for interpreting successional processes that to some extent modify or rejuvenate the secondary succession, interrupting successional stages and avoiding the formation of homogeneous steady states. The phase difference or maturity is the time lag since the last disturbance event. Other local random events can overlap phase differences, creating a more diverse environment. Also, a moderate disturbance regime increases the heterogeneity, but this behavior is quite different compared to starting the environment's ontogenesis.

## 5.2.2 Scale and ecological neighborhoods

Heterogeneity is a concept applicable to any scale of the landscape. A system can have higher or lower heterogeneity according to the resolution by which it is observed.

A patch may be defined as a discontinuity in environmental character states. Environmental patterning assumes great importance for most of the ecological processes. Heterogeneity means that there are almost two different patch types which are different in suitability. Three main categories of spatial aggregation have been recognized by Addicot et al. (1987) as divided homogeneous, undivided heterogeneous, and divided heterogeneous (Figure 5.3). In the first case, we can assume than suitable patches for a species are imbibed in a matrix of unsuitable medium such as the sea for insects. In the second and third cases, the undivided heterogeneous shows a different quality of patches. In the last case,

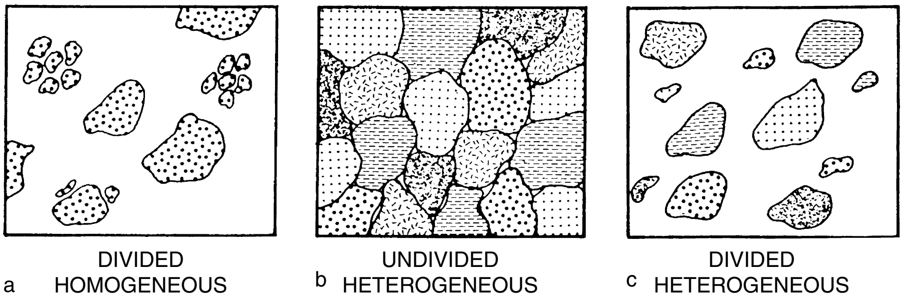

*Figure 5-3*. Possible combination of patchiness in a heterogeneous landscape (from Addicott et al. 1987, with permission).

there are patches of different quality interspersed in an unsuitable environment. For example, fire, grazing and the combination of these two disturbances were tested at local and regional scales in the tall grass prairies of northeastern Kansas by Glenn et al. (1992). Disturbance in tallgrass prairies had different effects according to the spatial scales. Burning was producing more heterogeneity at a local scale and grazing seemed more efficient at the regional scale (15 × 15 km).

At a local scale (0.1 ha), the undisturbed control plot was more heterogeneous than all other treatments. Regional responses to disturbance were more unpredictable than local responses.

Spring burning opened dense grass cover, facilitating the germination of seed banks. Grazing after burning maintained open spaces, favoring the implantation of rare species. Burning in fall decreased species diversity and this was depended on the poorer seed bank. High heterogeneity at the regional scale of burned or graze-burned treatments, was probably dependent on the effect of species dynamism in time and space. The patchy character of an environment creates more difficulties in the choice of the spatial and temporal scale of investigation.

Patchiness is not always important for the entire ecological process and the responses of organisms seem an appropriate criterion to scale the environment. In order to find a criterion to measure environmental patterning, it seems useful to introduce the concept of neighborhood for an organism, as the region within which that organism is active or has some influence over an appropriate period of time. The neighborhood dimension is linked to the organisms and the ecological processes that have been selected for this comparison.

Using the neighborhood concept it is possible to measure the relative size, isolation and duration of patches. The fine or coarse grain appears as a matter of neighborhood characters. Thus, if a patch is too large for a neighborhood, then that organism uses that patch in a coarse way. To estimate the neighborhood size, a great variety of indicators can be used, but for vagile organisms, the net movement of individuals seems appropriate. For sessile organisms, the neighborhood size can be estimated according to the regions from which food, predators and mutualistic foragers are coming.

This approach seems very promising because scaling neighborhoods means scaling processes interacting with that organism.

### 5.2.3 Disturbance and heterogeneity

According to Risser (1987), the role of heterogeneity in the disturbance regime can be controversial. In fact, in some cases, heterogeneity can interrupt the spreading of a disturbance such as a fire in a mixed woodland in which the flammability of coniferous species is higher than that of broadleaves. In other cases, as in agroecosystems in which woodlots are interdispersed in a matrix of cultivation, deer that find suitable habitats in woodlots can disturb the surrounding crops.The non-random distribution of species across scales mainly depends on the community heterogeneity (Collins 1992). Larger samples include a higher number of species than small samples; so we expect a higher similarity in larger plots rather than in small ones.

Heterogeneity was negatively correlated with burning frequency in Konza Prairies (Collins 1992) (Figures 5.4 and 5.5). Mean annual heterogeneity on annual burned grasslands was always less than the unburned plots. In this case,

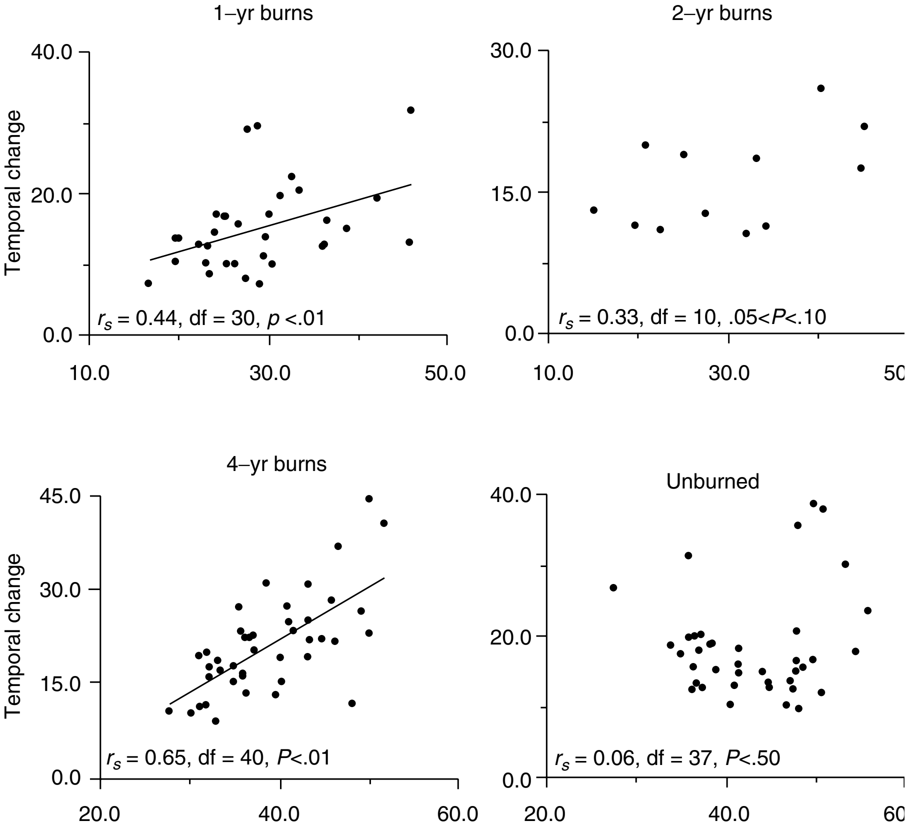

*Figure 5-4*. Spearman rank correlation of within-site heterogeneity in species composition, in a given year and proportional change in species composition (from Collins 1992, with permission).

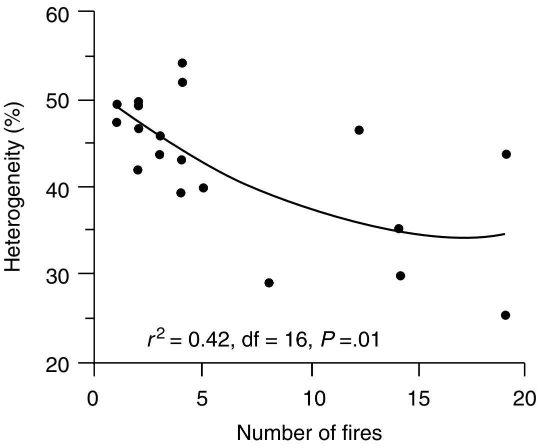

*Figure 5-5*. Relationship between number of times a site has been burned between 1972 and 1990 and site heterogeneity in 1990 (from Collins 1992, with permission).

an intermediate disturbance regime decreases the heterogeneity. Spatial and temporal heterogeneity are positively correlated at one years' and four years burning frequency.

### 5.2.4 Heterogeneity and animals

With this title "Spatial heterogeneity and animals" Levins (1968) open a chapter of his booklet *Evolution in changing environments* dealing mainly on the genetic consequences of patchy environments according to the way in which an animal perceives the environment as fine or coarse grained.

For instance, spatial heterogeneity, measured as horizontal variability in the type profiles in a habitat, has been recognized as one of the major factors influencing bird diversity (MacArthur et al. 1962). Roth (1976) found a good relationship between an index of heterogeneity and BSD (Bird Species Diversity). But as the trees became denser, tree and shrub canopies had less influence on heterogeneity. Scattered trees and shrubs were more important to assure habitat patchiness.

But Percentage Community Overlap (PCO) as % of the entire community, which is expected to overlap at a given site, is negatively correlated with BSD (Roth 1976) (Figures 5.6 and 5.7). Patchiness can be used to explain the differences in diversity between sites of the same habitats. The higher bird diversity in shrubby habitats probably depends on the highest shrub heterogeneity compared with low diversity in tree habitats, although they have more vegetation layers or volume.

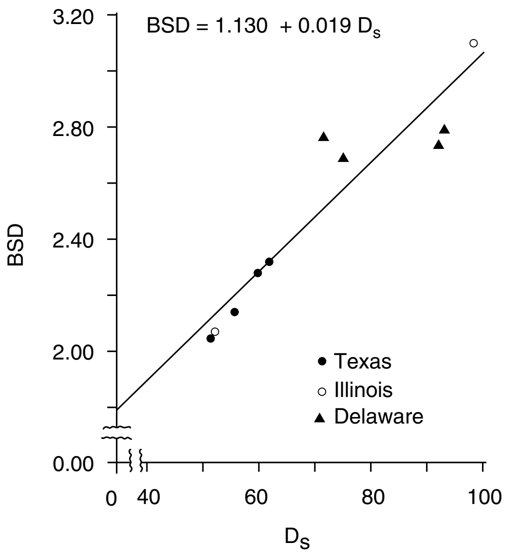

*Figure 5-6*. Index of heterogeneity (Ds) and bird species diversity (BSD) for shrublands and forests in Texas, Illinois and Delaware (from Roth 1976, with permission).

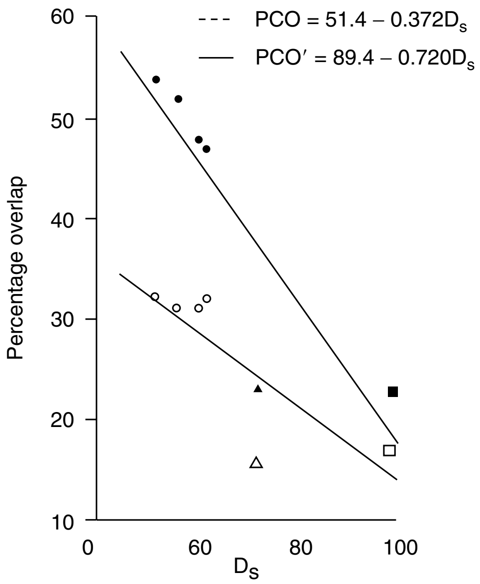

*Figure 5-7*. Index of heterogeneity (Ds) and % overlap (PCO and PCO') for Illinois Forest-Edge (squares), Texas brushlands (circles), and UD Woods (triangles) (from Roth 1976, with permission).

It is also quite clear that vegetation physiognomy is not enough to explain animal distribution but that floristic composition also plays an important role (Rotenberry 1985).

The landscape context (i.e., the typology of surroundings of a select habitat patch) has found important components to support the diversity of bird assemblage in coastal wet meadows, as reported by Riffell et al. (2003). The distribution pattern of water voles (*Arvicola terrestris*) is related to landscape composition and structure, as investigated by Duhamel et al. (2000).

Recently, Butler (1995) reviewed the role of animals as geomorphic agents and although no explicit reference was made to the heterogeneity, in his presentation it appears quite clear that animal effects have to be considered as increasing factors of spatial heterogeneity.

Invertebrates such as ants and termites, vertebrates such as shorebirds, mammals such as beaver, buffalo, rodents and moles are building, burrowing, digging, trampling and moving soil and opening vegetation cover.

Domestic livestock, when densely reared, can permanently modify the vegetation cover, producing a new landscape. An example for all is represented by the terracettes on the mountain pastures, produced on steep slopes by sheep and goat trampling.

For instance, the savanna vegetation in Zimbabwe is patterned at various scales (Scoones 1995). At a regional scale is the rainfall gradient and geomorphology. At the landscape scale is the disposal of soil types. At microscale, vegetation and heterogeneity are dominated by slope, soil type and vegetation disturbance regime.

To maintain resources in savanna grazed by cattle, wild animals and goats, it is important to understand the mechanism of working at different scales has the capacity to reduce competition and maintain the heterogeneity of the vegetation patches, assuring the resilience of the system. Scoones argues for the necessity to ensure opportunistic and flexible movements at different scales between resources.

Spatial heterogeneity definitely affects the rate of movement and tortuosity in herbivorous animals, as documented by Etzenhouser et al. (1998), studying the foraging behavior of two browsing ruminants: white-tailed deer (*Odocoileus virginianus*) and Spanish goat (*Capra hircus*). Tortuosity was found to be higher in Spanish goats. The two species have been found to perceive the same landscape differently.

Spatial heterogeneity has been found to be affected by migratory grazers in the Yellowstone National Park by Augustine & Frank (2001), especially at the scale <10 cm. This effect has been attributed to the grazing activity of wild grazers that increases the plant diversification. This apparently disagrees with the predictions that heterogenity in grazed areas largely depends on dung and urine deposition. Soil N seems to be affected by grazers at a scale of 5–30 m, when compared with the distribution in ungrazed areas that do not show spatial structure.

### 5.2.5 Spatial heterogeneity and prey-predator control system

Spatial heterogeneity can be responsible for some spatial density dependence (Dempster & Pollard 1976). If prey are patchily distributed and the predators tend to concentrate in patches of high prey density, the predator population flourishes, while areas with low prey density temporarily function as refuges (May 1978, quoted by Dempster).

### 5.2.6 Foraging efficiency and heterogeneity

Animals can spend less time searching in large patches, than in small patches. In fact, the distance between patches varies linearly with the linear dimension of the patch, while hunting activity in the patch varies as a square. Larger patches are used in a more specialized way than small patches (MacArthur & Pianka 1966).

In large herbivores, like elk and bison, foraging in a sagebrush-grassland landscape in northern Yellowstone National Park, Wallace et al. (1995) found, during winter time, a response to heterogeneity only at broad scale (landscape) while at the fine scale ($30 \times 30$ m) the selection of patches was random. These results indicate that the species moves from one area to another area according to the abundance of biomass, but that locally, they move randomly. This behavior indicates that when these animals are inside a patch of foraging vegetation, no finer-scale choices are made and finally, that heterogeneity at the small scale is not appreciated. This probably allows them to save travel energy by moving randomly at a finer scale, but moving non-randomly at a broader scale, according to higher biomass concentrations.

But experiments on bighorn sheep conducted by Gross et al. (1995) in an artificial enclosure demonstrated a different mechanism; at a small scale in time and space, this species moves directly from one plant to the closest plant (75% of all moves). Here, 90% of all the moves were directly to the three closest plants and 75% of the time was spent moving directly from one plant to another.

Although a hierarchy in the choice of patch has been invoked by many ecologists, in this case, in which plants were visible, the closest-neighboring choice was relevant. So, are the responses of foragers to larger scales the summation of small-scale decisions? This is an intriguing point to be analyzed. Probably, heterogeneity can play a relevant role in the determination of the more efficient food intake strategy, especially in periods of food shortage (Figure 5.8).

In heterogeneous landscapes, animals move not in a straight line but are strongly conditioned by the spatial arrangement of the suitable-unsuitable

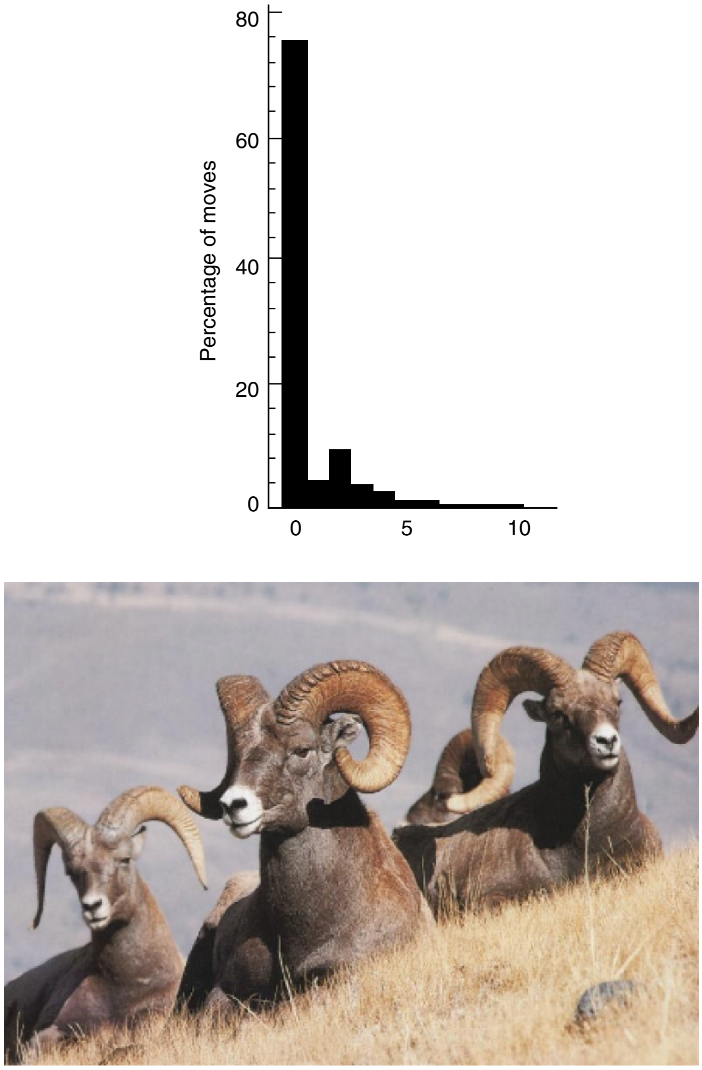

*Figure 5-8*. Percentage of moving according to plants ranked by their proximity to animals (bighorn sheep (*Ovis canadenis*)) (modified from Gross et al. 1995, with permission).

patches (Johnson et al. 1992) and it may be expected that their behavior would be affected by the spatial arrangement of suitable/unsuitable patches (Figure 5.9).

An example of apparent adaptation to heterogeneous landscape is presented by Root & Kareiva (1984), studying the movement of cabbage butterflies (*Pieris rapae*). This species places more eggs on isolated hosts than in dense stands. This adaptation to heterogeneous landscape is discussed in terms of a risk-spreading hypothesis.

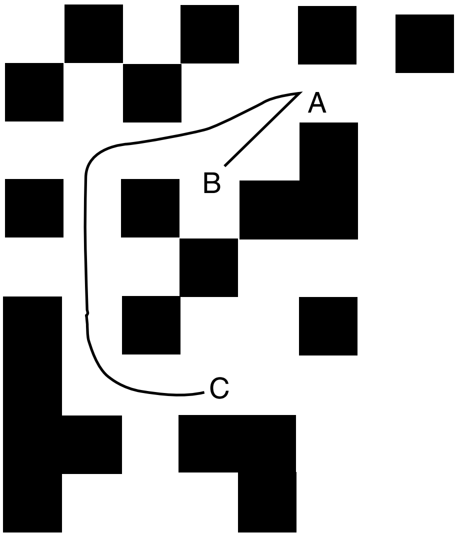

*Figure 5-9*. In heterogeneous landscapes, movement length and complexity are conditioned by the spatial arrangement of patches (from Johnson et al. 1992, with permission).

According to research by Plowright & Galen (1985), the pollinator flight of bumble bees foraging routes between plants of *Hieracium aurantiacum* is strongly influenced by the heterogeneity of the landscape. In a more uniform landscape, bumble bees fly farther. In areas in which landmarks have been removed, the number of backward moves was less than in areas with abundant landmarks, when the flight is more direct and the interplant flight distance significantly longer in uniform areas. Although it is not clear why this behavior is maintained, bumble bees, as other pollinator insects, are sensible to the visual landscape and heterogeneity.

Southwick & Buchman (1995) have found that the homing capacities of honey-bees were improved by heterogenous mountain landscapes and decreased in flat landscape. Honeybees use horizon landmarks to navigate across long distances. The homing success decreased with the increase of distance from the nest. In mountain landscapes, honeybees were capable to homing from 9 km, but in flat land, 5 km was the maximum distance from which this species returned (Figure 5.10).

### 5.2.7 Heterogeneity and migratory birds resource use

Forest gaps, important sources of forest heterogeneity, play a relevant role in oriented patch use for migratory birds (Martin & Karr 1986). In gaps, the foliage profile is significantly different that in no-gap sites (Figure 5.11). More

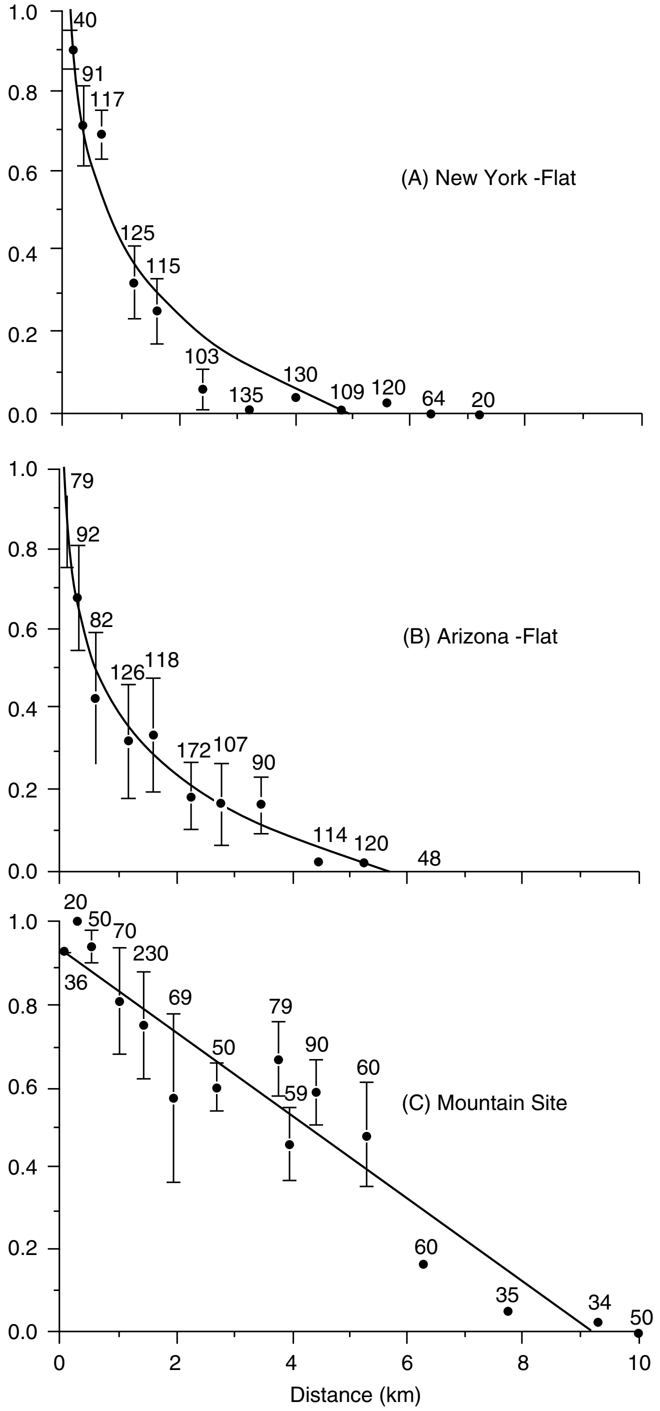

*Figure 5-10*. Percentage of recaptured foraging bees according to three different areas and different distances (from Southwick & Buchman 1995, with permission).

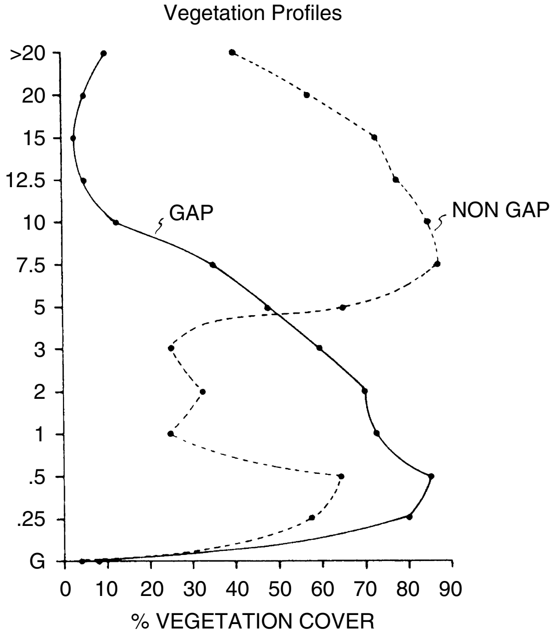

*Figure 5-11.* Vegetation profile of gap and non-gap areas. Gap areas are characterized by vegetation cover of the lower layers (from Martin & Karr 1986, with permission).

fruits have been found. Birds that use resources concentrated in gaps use more gaps than no-gap sites, although the use of a gap site by birds is not restricted to food availability but also to other factors such as perching sites and, ultimately the abundance of some vegetation profile close to the soil.

A gap can attract birds because there is more light. If the resources are abundant, birds can stay longer and accumulate abundance at that site. Mixed flocks can behave as a center of information for other individuals, especially for migrants that have no previous information on the resource location.

Finally, Martin and Karr (1986) have clearly found that bird distribution is consistent with resource abundance when resources are patchy.

### 5.2.8 Quantify spatial heterogeneity

Spatial heterogeneity can be defined as the complexity and variability of a system property in the space (Li & Rynolds 1994), where a system property can be soil nutrients, patch mosaics, plant biomass, animal distribution, etc.

The variation of spatial heterogeneity reflects the rate of change in functions and processes. Li & Rynolds (1994) argued the importance of producing a clear definition of heterogeneity in order to approach this landscape attribute with good quantitative tools.

These authors tested four indices to quantify spatial heterogeneity in simulated landscape maps according to five components of spatial heterogeneity (number of patch types, proportion of patch types, spatial arrangement, patch shape, neighboring contrast) (Figure 5.12) :

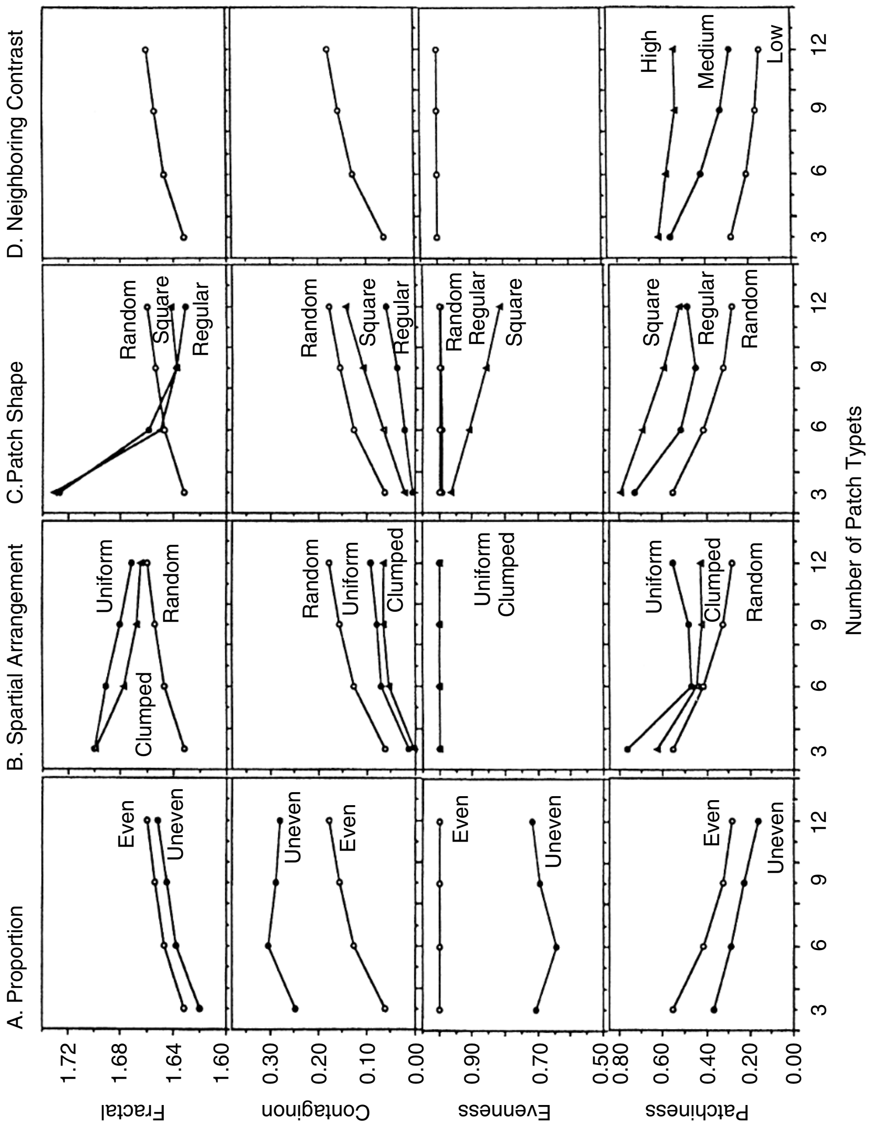

*Figure 5-12*. Responses of four indices of spatial heterogeneity (Fractal, Contagion, Evenness, Patchiness) to the five components of spatial heterogeneity (Proportion (Uneven, Even), Spatial arrangement (Uniform, Clumped, Random), Patch shape (Random, Square, Regular), Neighboring contrast (High, Medium, Low), using simulated landscape maps (from Li & Reynolds 1994, with permission).

(a) Fractal dimension. This index measures the complexity of the edges (Burrough 1986).
(b) Contagion. This index measures the extent to which patches are aggregated (O'Neill et al. 1988).
(c) Evenness. This index is sensitive to the number of patch types and their proportion in the landscape (Romme 1982).
(d) Patchiness. This index measures the contrast of neighboring patch types in a landscape mosaic (Romme 1982).

These four indices are to some extension correlated, and then show some redundancy, especially since the contagion and the evenness are highly correlated. But the correlation between the fractal dimension and these indices is weak. This means that the fractal dimension is recommended to be used in combination with the other indices (For more details on these indices see Chapter 8).

## 5.3 ECOTONES

### 5.3.1 Introduction

Recently, the heterogeneous character of the landscape (mosaic) and the influence of the spatial arrangement of the composing patches of many ecosystemic processes have been recognized (Pickett & White 1985; Hansen et al. 1992). Patches have been considered as entities distinct from a background. The distinctiveness of patches obliges us to recognize a portion of inter-patch space with an intermediate character or with a unique character, completely different (Figure 5.13).

*Figure 5-13*. (A) woodland ecotone between *Quercus ilex* (darker) and *Quercus pubescens* (lighter). The ecotone appears as a mixture of the two species, although it is probable that *Quercus pubscens* will move into *Quercus ilex s*tand (Tergagliana Mt, northern Apennines, Italy).

The process of recognition of patches is linked to Individual-Based Landscape (IBL) or Observed-Based Landscape (OBL). For this it is possible to classify a Neutrality-Based Landscape (NBL) to the two approaches and to define the patches. In other words, is it possible to classify the same area in different ways according to the approach used, the focal species or process, or simply according to the scale of resolution. For the same reason, boundaries between patches exist in different positions and with different characters. Boundaries mark the limit between patches and assume the characters of complex and multidimensional entities. We have included that such boundaries, which were called ecotones a century ago in the chapter devoted to patterns, although boundaries develop intense and primary functions in the landscape mosaic. Boundaries can be interpreted like passive or active filters, but also relevant drivers in a mosaic theory. The identification of patches and boundaries is based on the research question (Cadenasso et al. 2003) (Figure 5.14) and also by the epistemological framework adopted. Boundaries between patches have been named in different ways: edges, ecotones, boundary layers, gradients, clines, transition zones, interfaces (see also Lidicker 1999, Burel 1996). We will use these terms indifferently, considering such synonimous terminology. The term ecotone has been preferred in this esposition: Ecotones were described by Clements (1905) as tension zones where principal species from adjacent communities meet their limit. Later, Odum (1959) again stressed the importance of defining a transition zone between two communities. Ecotones are situated where the rate and the dimension of ecological transfers (solar energy, nutrient exchange) have an abrupt change compared with the behavior of the interior of the patches.

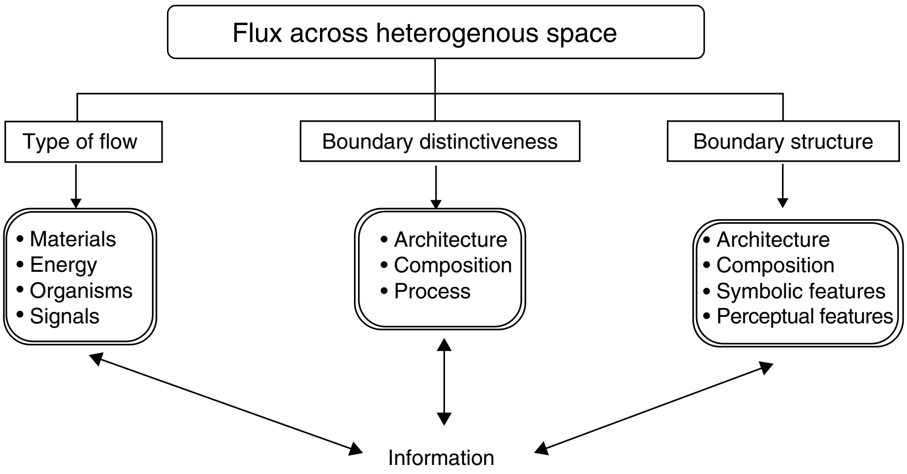

*Figure 5-14*. A conceptual framework for the ecological boundaries (modified from Cadenasso et al. 2003b).

An ecotonal community has species common to both the communities that overlap with organisms typical of the edges. The tendency to have a high number of species was called the edge effect by wildlifers. The ecotone may be considered a true habitat but also a frontier habitat (Ricklefs 1973) where the habitat overlap encourages species diversity (Harris 1988).

### 5.3.2 The importance of ecotones

Ecotones are important key structures for the functioning of landscapes; nutrients, water, spores, seeds and animals move across these structures and today play a preeminent role as indicators of climatic changes due to $CO_2$ doubling and air pollution. Ecotones, although of reduced space in the landscape mosaic, contribute to regulate flows across heterogeneous spaces.

The high biological diversity present in the ecotones, the contribution to the system integrity, the high rate of primary and secondary production are other relevant attributes.

Recently, Smith et al. (1997) have attributed a primary role to ecotones in generating rainforest biodiversity, locating ecotones like sources of evolutionary novelty (Figure 5.15). Also, Burel and Baudry (1995) have recognized a social, aesthetic and ecological role in rural landscapes.

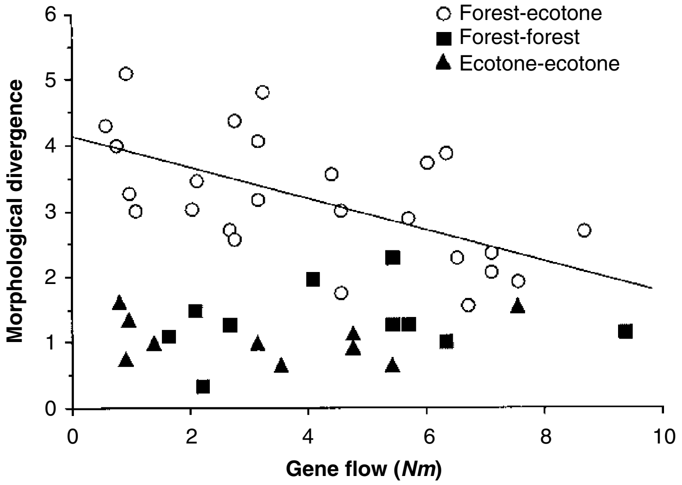

*Figure 5-15.* Relationship between gene flow and multivariate morphological divergence occuring in different landscape components inside tropical forests. Open circles represent pairwise comparisons betwen populations in forest patches occurring in the ecotones and contiguous forest populations. Solid triangles represent populations occurring in the forest patches within the ecotone. Solid squares represent populations occurring in the contiguous forest (from Smith et al. 1997, with permission).

Many data is available on ecotones from different parts of the planet but this information is not organized enough to assure an efficient comparison. Consequently we need more experimental data and affordable models.

In man-modified ecosystems, ecotones are the sites with high environmental diversity (woodlots, edges, tree belts) and refuges for rare or human disturbance regime-sensitive species.

Long rivers, lakes and coastal lagoon ecotones control the flux of water and nutrients that move from terrestrial to aquatic ecosystems and *vice-versa*.

New methods to detect boundaries, metrics and modeling are popular themes of the more recent studies (Fortin et al. 2000; Peters 2002; Fagan et al. 2003).

### 5.3.3 Concepts and definitions

Many authors have considered edges as important sites to study natural communities (Clements 1897; Livingston 1903; Griggs 1914). Clements (1905) was the first ecologist to introduce the word ecotone (a Greek word) composed by Oikos (household) e Tonos (tension). Later, Shelford (1913) and Leopold (1933) confirmed the observation that species richness was higher long ecotones. Since that time, the majority of scientific writers has stressed their importance (Weaver & Clements 1928; Odum 1959; Daubenmire 1968; Ricklefs 1973). Recently, many authors have recognized the importance of studying ecotones (Risser 1995; Holland 1988; Naiman et al. 1988; Holland et al. 1991) and important fora have been organized by UNESCO, Scientific Committee on Problems of the Environment (SCOPE) and by the Council of Scientific Unions (ICSU), to discuss the ecological and management components of ecotones (Table 5.1). At least six significant publications have been produced : *A new look at ecotones ( Di Castri et al. 1988), The ecology and management of aquatic-terrestrial ecotones (Naiman & Decamps 1990), Ecotones. The role of landscape boundaries in the management and restoration of changing environments (Holland et al. 1991), Landscape boundaries. Consequences for biotic diversity and ecological flows (Hansen & Di Castri 1992), Understanding and managing ecotones (Risser 1995), Buffer zones: Their process and potential in water protection (Haycock et al. 1997).*

The Ecological Society of America has devoted an issue of Ecological Applications (3(3), 1993) Risser (1993) on the ecotones and their scaled properties and, more recently, a special session has been dedicated to the ecological boundaries by BioScience (53(8), 2003) (Cadenasso et al. 2003a). The first textbooks of landscape ecology have reported this subject extensively (Forman & Godron 1986; Farina 1993; 1995; Forman 1995).

The ecotones are transitional zones between different habitats, exist at all spatial and temporal scales (Delcourt & Delcourt 1992, Rusek 1992) and are created and maintained by a hierarchy of tension factors such as air mass

*Table 5-1.* Definitions, functions, time and spactial scale and factors shaping ecotones.

| |
|---|
| *Definitions:* |
| 1. Sites in which energy exchange and materials are highest |
| 2. Transition sites between different habitats |
| 3. Tension zones between systems at different maturity |
| *Functions (ecotones as cellular membranes):* |
| 1. Passive diffusion |
| 2. Active diffusion |
| 3. Filter or barrier |
| 4. Accumulation |
| 5. Sink |
| 6. Source |
| 7. Habitat |
| *Spatio-temporal scales and ecotones* |
| Spatial scale: |
| 1. Micro-ecotone |
| 2. Meso-ecotone |
| 3. Macro-ecotone |
| 4. Mega-ecotone |
| Temporal scale: |
| 1. Ephemeral |
| 2. Seasonal |
| 3. Permanent |
| *May be produced by* |
| Exogen factors: |
| 1. Topography |
| 2. Climate |
| 3. Hydrography |
| Endogen factors: |
| 1. Ecological succession/competition |
| 2. Disturbance |
| 3. Stress |
| 4. Human activity |

dynamics, mega-topography, local geomorphology, disturbance, competition, plant growth and development. Tension areas are places in which two organizations meet and exchange the components or where genetic stresses are at work.

Often ecotones are of a functional type and are particularly important for the areas that separate sub-systems with a different degree of maturity (Margalef 1968).

Among the different possibilities to study ecosystems, focusing attention on ecotones where the energetic exchanges and materials have a high level, represents a meta-systemic approach, typical of landscape ecology (Wiens et al. 1985). In fact, the diversity and abundance of species (Noss 1983; Imaz et al. 2002), flux and accumulation of materials and energy (Ranney et al. 1981) and the disturbance diffusion (Pickett & White 1985), are strongly influenced by the borders of the land mosaics. Thus the functioning of a landscapes needs ecotones, giving these structures a central role to understanding the ecological processes (Hansen et al. 1992).

In terrestrial ecosystems, ecotones are seen as soil or vegetation discontinuities, while in heterogenous systems, ecotones are the borders of patches forming the land mosaic. The reduction of ecotones for cropland intensification is one of the causes of biodiversity decline (Pogue & Schnell 2001). Marini et al. (1995), studying the forest-farm edge in Southern Illinois, have found that at the edges, predation was higher and argued that in the study area edges represent traps for breeding birds.

The environmental conditions can change abruptly, like between a field and a wood, or between the riparian vegetation and the desert or in a more gradual way from a forest to a mountain prairie by crossing intermediate shrub cover.

Ecotones have been considered by Forman & Moore (1992) as cellular membranes, functioning as filters, assuring active and passive transportation according to energy fluxes or type of materials.

The presence of ecotones in an environmental system is of fundamental importance for the functioning of the entire system. In fact, the traditional ecology has focused the investigation at the interior of homogenous patches in order to reduce the internal variability and the external influences while landscape ecology, considering the globality of a system, has to face structural or functionally defined entities that create the discontinuity of the system (Figure 5.16).

From the first definitions of transitional zones between communities, ecotones have been defined as “Zones of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems” (Di Castri et al. 1988).

Ecotones could also be considered an area in which some processes reach the limit of their performance and ecotones become critical areas for survival or for the diffusion of organisms like the alpine treeline where, for instance, tree seedlings are rare and where snowpack depth is the driver of seed abundance, as documented by Hattenschwiler & Smith (1999) along the Medicine Bow Mountains (Wyoming, USA), see also Camarero et al. (2000). The ecotone paradigm can be used to better understand the biogeographic tension zone when distributions of species are considered to be indicators. For instance, Naranjo et al. (1998) have utilized ascidians to understand the faunal differentiation across Atlantic-Mediterranean coasts (Figure 5.16).

### 5.3.4 Difficulties in studying ecotones

Due to their temporary characters and scaling properties, ecotones are components of a landscape that are hard to investigate (Martinez & Fuentes

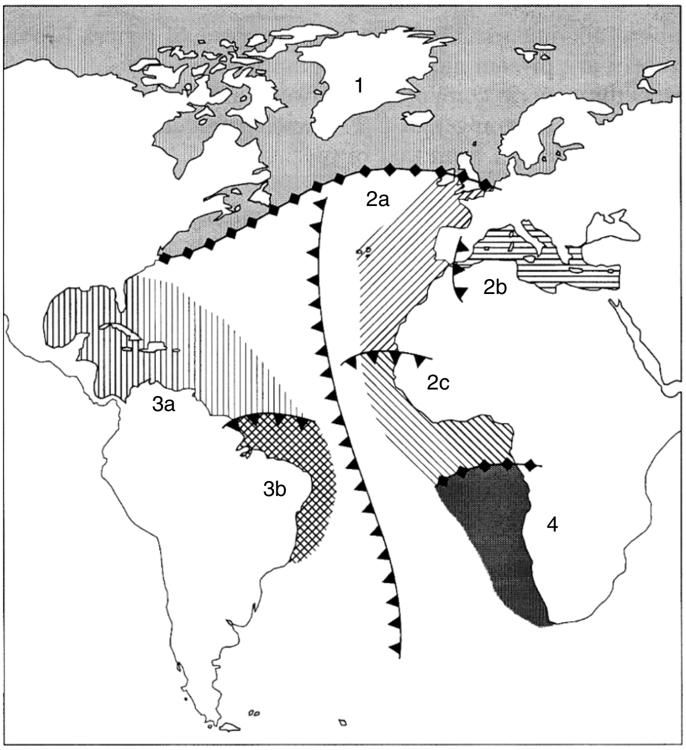

*Figure 5-16*. Location of tension zones across Atlantic-Mediterranean coasts by using Ascidians as indicators of faunal changes. Differences in species are indicated by teeth, genera by double teeth. Faunistical regions: (1) Northern Atlantic, (2) Mediterranean Atlantic Region (2a=Lusitanico-Mauretanian area, 2b=Mediterranean; 2c=Tropical West African); (3) Central Western Atlantic Region (3a= Caribbean area; 3b=Brazilian area); (4) South Eastern Atlantic (from Naranjo et al. 1998, with permission).

1993). Their distinctive patterns vanish when closely observed because they are scale dependent, as argued by Margalef (1968). In fact, the structure and functions of ecotones in many cases are not related to physical patterns, especially when the ecotones are created by human disturbance regimes. The presence of an ecotone is species-specific and also all characters of ecotones are not absolute but relative to the target species perception of the surroundings (Shugart 1990).

The localization and the size of ecotones are two main points; generally, an edge is considered to be where the contrast between patches is maximum.

Using this approach, Turner et al. (1990) have studied the variations of annual and perennial vegetation, ants, lizards, birds and mammals along a transect 2700 m long, sampling every 30 m and comparing pairwise sampling, aggregating the samples until reducing the samples to a pair (Figure 5.17).

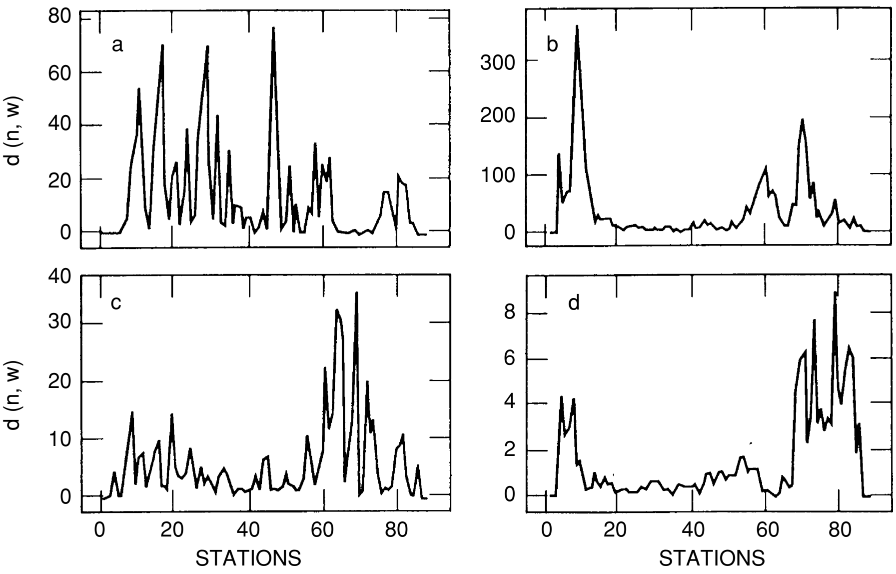

*Figure 5-17.* Ecotones intersected by a) ants, b) mammals, c) lizards and d) birds in a grassland. The peaks of differences between the samples indicate discontinuities in the resources or habitats, the peaks are species-specific (from Turner et al. 1990, with permission).

The ecotones are structured through the encounter with patterns and processes; in this case ecotones are contemporary boundaries (*sensu* Strayer et al. 2003). When processes are no longer operating at that site, ecotones are considered to be relict boundaries. And it is often difficult to classify contemporary or relict ecotones, because a mixture of current and past forces are still active.

### 5.3.5 Spatio-temporal scales and the hierarchy of ecotones

The complexity of ecological systems can be observed from a hierarchical approach in which every system is composed of a set of nested subsystems (Allen & Starr 1982; O'Neill et al. 1986; Allen & Hoekstra 1992), distinguished by different spatio-temporal scales (Delcourt et al. 1983; Delcourt & Delcourt 1987, 1988; Brubaker et al. 2001).

Ecotones representing the boundaries of different ecological systems exist at all scales (Belnap et al. 2003) and, as ecological systems, they can be classified into mega, macro, meso and micro ecotones. Gosz (1993) distinguished five hierarchical levels for the ecotones: biome ecotone, landscape ecotone, patch ecotone, population ecotone and individual ecotone (Table 5.2).

*Table 5-2*. Hierarchical organization of ecotones and variables that create the gradient or constraint on which ecotones exist.

| Ecotone hierarchy | Probable constraints |
|---|---|
| Biome ecotone | Climate(weather) + Topography |
| Landscape ecotone | Weather + Topography + Soil characteristics |
| Patch ecotone | Soil characteristics + Biological vectors + Species interaction + Microtopography + Microclimatology |
| Population ecotone | Interspecific interactions + subtitute intraspecific interactions + Physiological controls + Population genetics + Microtopography + Microclimatology |
| Plant ecotone | Interspecific interactions + Intraspecific interactions + Physiological controls + Plant genetics + Microclimatology + Soil chemistry + Soil fauna + Soil microflora, etc. |

The higher level of this classification is represented by the biome ecotone, formed by the blending of patches of different shape and size belonging to two adjacent biomes.

The second level is represented by the environmental mosaic or transition zone in the shape and size of the patches of every biome. The third level is the transition zone between patches, composing a biome.

The fourth level is represented by the transition among populations. This ecotone exists when a species has a patch distribution.

The fifth level is represented by the ecotone created by an individual (plant) forming a zone of transition due the combined effect of competition for nutrients, water and light. The number of variables that create the ecotonal gradient increases in proportion to the finest level of scale.

If we consider the temporal scale, we can see that at the scale, of $10^4$ years the ecotones are created by the vegetation shift according to the climatic changes. At a scale of $10^3$ ecotones are created by the effects of different disturbance regimes of replacing civilizations. At a scale of 100 years, ecotones are created by coastal and river network dynamics.

At an annual scale, ecotones are created by a flooding regime. At a seasonal scale, ecotones are produced by a climatic event such as snow melting and the availability of water in the soil. At a daily scale (ephemeral), ecotones can be created by thermal constraints in the soil.

A landscape can be homogeneous at a scale, without ecotones, and heterogeneous at another scale, presenting ecotones (Meentmeyer & Box 1987).

Risser (1987) introduced some principles important to understanding the functioning of an ecological system, related to the presence and functioning of the ecotones:

a) The relationship between structures and processes is not limited to a unique spatio-temporal scale.

b) The importance of a process is scale dependent. For instance, a biogeographical process has a negligible effect on local patterns but is important at a broad scale. This is the example of local extinction compared with the geographical range of a species.

c) Every group of plants and animals is connected with the environment at a species-specific scale. Every species has a specific perception of the environment.

d) The scale of the ecological system is established by the goal of the research. Some structures and processes are not perceived if the resolution of the investigation is coarser (O'Neill et al. 1986).

### 5.3.6 Ecotone classification

Ecotones exist at all scales and the attempt to classify could seem too artificial, but the classification of ecotones recognizable at the human scale assumes a relevant importance from a management perspective. The main attributes of ecotones are summarized in Table. 5.3.

Ecotones may be created by natural or human-induced interactions.

Holland (1988) shows a scheme of classification:

a) Ecotones created and maintained by human disturbance regimes (shelter belts).

b) Ecotones created and maintained by natural processes (the flooded areas by beaver digging).

c) Ecotones produced by natural processes and maintained by human activity (a strip of riparian forest maintained by man).

d) Ecotones created by human activity and maintained by natural processes (flooded area around artificial reservoirs).

#### *5.3.6.1 Horizontal and vertical ecotones*

Most of the information available on ecotones regards the spatial arrangement of the patches. Implicitly, the vertical ecotones have also been considered important. Since 1961 (MacArthur & MacArthur 1961), bird diversity was compared with the complexity of the vertical structure of the vegetation. A typical vertical ecotone is represented by the thermic behavior of soil, water and air mass. But ecotones can also be observed in the soil humidity (Figure 7.18) and in the turbulence of hazes in the troposphere.

#### *5.3.6.2 Natural versus human-induced ecotones*

Ecotones produced by natural processes have a soft gradient (Hobbs1986), while the ecotones produced by human disturbance regimes have a sharp gradient and the transition zone is often structurally nonexistent.

*Table 5-3*. Main attributes of ecological boundaries (from Strayer et al. 2003, with permission).

How did the boundary originate, and how is it maintained?
- Investigative or tangible
- Casual or consequential
- Contemporary or relict
- Endogeneous or exogeneous origin
- Endogeneous or exogeneous controls (maintenance or suppression)

What is the spatial structure of the boundary?
- Grain size
- Extent
- Thickness and dimensionality
- Geometry of adjacency
- Interactive or noninteractive
- Abruptness, steepness
- Patch contrast
- Integrity (perforated versus unbroken)
- Geometric shape and turtuosity
- Number of attributes (single or multiple)
- Offsets or congruencies of multiple attributes

What are the functions of the boundary?
- Transformation
- Transmission
- Absorption
- Amplification
- Reflection
- Neutral

How does the boundary change over time?
- Changes in any structural or functional properties
- Mobility (stationary, directional, oscillating, or random)
- Age and history

Natural ecotones are sensitive to climatic change and shift in land use, and can be profitably used as monitoring areas (Sullivan 2000), human induced ecotones can be used as indicators only indirectly for the influences of climatic change on human activities.

Human activity produces an alteration of the spatio-temporal scale of natural processes. In such a manner, logging produces the same effect as a natural forest gap by tree fall, but across mechanisms that are moving at different scales. In other cases human activity has produced modification and perturbations of natural systems that cannot be observed in natural systems such as the urban cover and other infrastructures such as paved roads and railways.

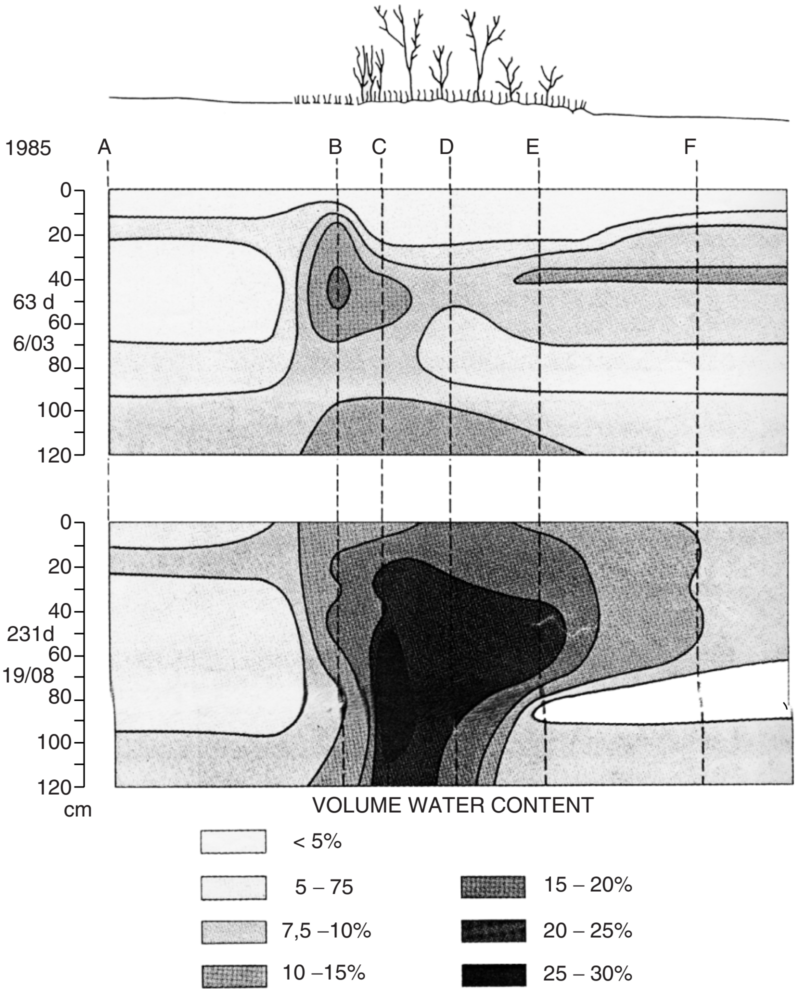

*Figure 5-18*. Vertical ecotone in desert vegetation stripes. Soil moisture at two different dates (March 6th, showing the peak of the dry season, and August 16th after 50.2 mm rainfall (from Cornet et al. 1992, with permission).

### 5.3.7 Structural and functional character of ecotones

The ecological boundaries between patches, that may be wide or narrow, are tridimensional structural and functional entities, in which the evinronmental contrast is steeper that in two adjoining systems.

To better understand the structure, dynamism and functioning of ecotones it is necessary to analyze their formation, maintenance and the inherent and extrinsic factors that assure their functioning (Figures. 5.19, 5.20).

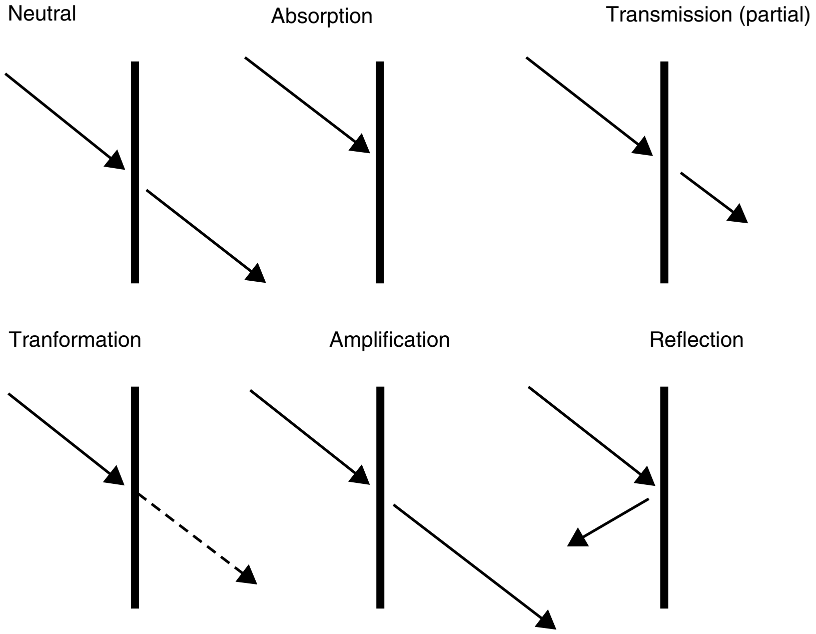

*Figure 5-19*. Behavior of processes at the ecotones. The heavy line is the ecotone (boundary), the thin arrows are fluxes across it. The length of the arrow indicates the size of flux (from Strayer et al. 2003, with permission).

The variables that take part in the formation and maintenance of an ecotone can be distinguished into structural and functional types.

The structural variables are size, shape, biological structure and structural constraint (Figure 5.21):

Size - the surface or the volume of the ecotone in respect to the size of neighboring ecological systems and the spatial scales of the fluxes between the ecological systems.

Shape - linear or circular or convoluted, etc. This variable seems more and more relevant to determine the rate of transfer of information, energy and material across ecotones.

Biological structure - the distribution of biomass or density of dominant organisms.

Structural constraint - the amount of difference between the biological structure of the ecotone and the adjacent ecological systems.

Internal heterogeneity - variance of the changing rate across a discontinuity.

Density - the length of ecotone per unit of land mosaic.

Fractal dimension - rate of complexity of the ecotone shape across a land mosaic.

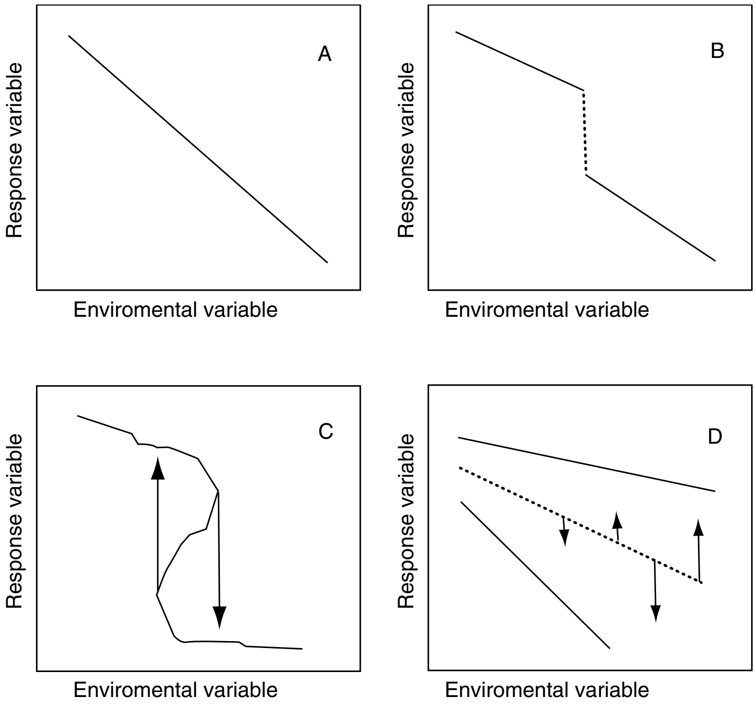

*Figure 5-20*. Reaction of an ecological system to an environmental variable: a. gradual; b. discontinuous; c.hysteretic; d. multiple responses (Shugart 1990, with permission).

Patch diversity - richness and evenness of patch types in the land mosaic.

Mean patch size - mean size of patches in a land mosaic.

The functional variables are: stability, resilience, quantity of energy and functional contrast.

Stability - it is the degree by which an ecotone resists the change when affected by a stress.

Resilience - it is the degree to which the ecotones return to an initial condition after stress.

Energetics - it is the productivity of dominant organisms, the flux of material and energy between the ecotones and the surrounding ecosystems.

Functional contrast - it is the extent of the differences of functional variables between the ecotones and the neighboring ecosystems.

Porosity - it is the capacity of an ecotone to change the rate or the direction of an ecological flux.

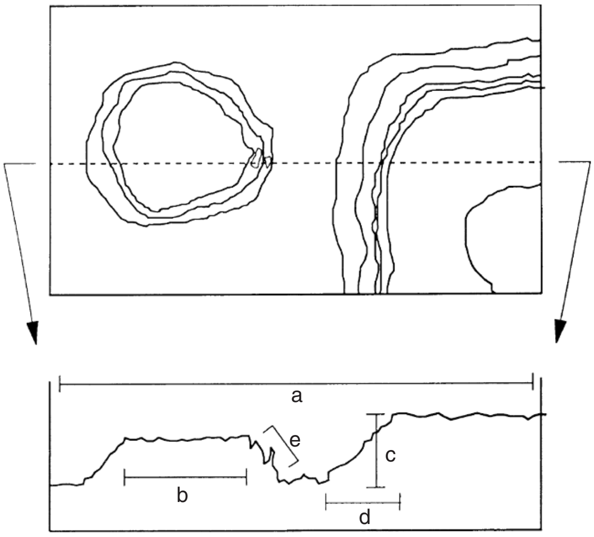

*Figure 5-21*. Some relevant characters of ecotones: (a) density (number of ecotones per unit distance or area); (b) width of adjacent patch; (c) contrast; (d) ecotone width; (e) internal heterogeneity (from Hansen et al. 1992, with permission).

### 5.3.8 Exogen controls for the creation and maintenance of ecotones

In the natural system, an edge can be created by external mechanisms that control the ecological systems or by internal discontinuities that are acting in the same system.

The environmental responds to the changes along a gradient, which may be gradual or linear. The response can show an abrupt interruption, probably due to a response with a threshold of one of the components composing the ecological system.

An abrupt change along the gradient of a system may originate at different levels of organization of the system.

A sharp gradient may occur when a species reaches the tolerance limit, for example, as a response to environmental variables such as temperature, salinity and pollutants in the soil. In other conditions, the abrupt change can occur in the biological responses from one species to another due to changes in competition. The response may be more complex and this condition mainly depends on the history and the evolution of the system and on the hysteretic relationship between the response and control variables.

Gradual responses to environmental gradients are very common in nature. For instance, the succession from open grassland to forest may cross many intermediate shrub-dominating stages (Figure 5.22).

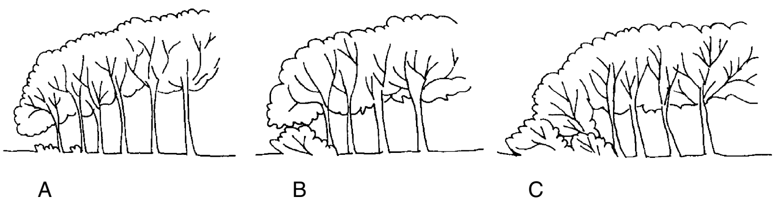

*Figure 5-22*. Three types of edge profile. The profile A is sharp without a shrub layer, B shows the presence of a shrub layer, and finally C is a complex profile with dense shrub cover coupled to small trees. These profiles affect animal presence and wind-dispersed and animal-dispersed plants (from Sarlov Herlin & Fry 2000, with permission).

### 5.3.9 Intrinsic controls in the creation and maintenance of ecotones

Edaphic, microclimatic and external disturbance, human disturbance included, affect or create ecotones, but it is reasonable to admit that internal factors are also able to oversee their maintenance (Odum 1990). Some of these factors are related to species-specific behavior. This situation has been widely documented in salamanders living in streamside environment, where larger species of genus *Desmognathus,* exclude the smallest of the genus *Plethodon* that move into a more dryer and less favorable habitat (Grover & Wilbur 2002). These authors have manipulated the environment by providing artificial seeps at various distances from the streamside in experimental plots in order to test the distribution of salamander along an ecotone. The distribution of animals is strongly related to the aggressiveness of the larger species (*Desmognathus fuscus* and *Gyrinophilus porphyriticus*) that displace *Plethodon cinereus* and *P. glutinosus* in dryer habitats (Figure 5.23). *Desmognathus fuscus* remained in distant plots 22 months after the seep treatment was interrupted and the habitat had returned to pretreatment conditions. In plots distant from the streamside and rarely visited by the dominant species, experimetally providing seeps and cover positively influenced the presence of *Plethodon cinereus*, confirming the hypothesis that a heterogeneous environment can be beneficial for subordinate, fugitive species that can exploit the portion of habitat that offers ephemeral opportunities.

In plants, some species have the capacity to exclude other species, creating a hostile environment. Mosses have the capacity to modify the pH of the interstitial water, preventing the colonization of other plants and creating in such a way a long duration steady state. In fact, the high acidity of the water that is in contact with mosses (pH 3-6) prevents the growth of other plants.

An ecotone can be maintained by the reproductive aggressiveness of some plants that rely on a dense crown, thick root systems or high biomass to prevent

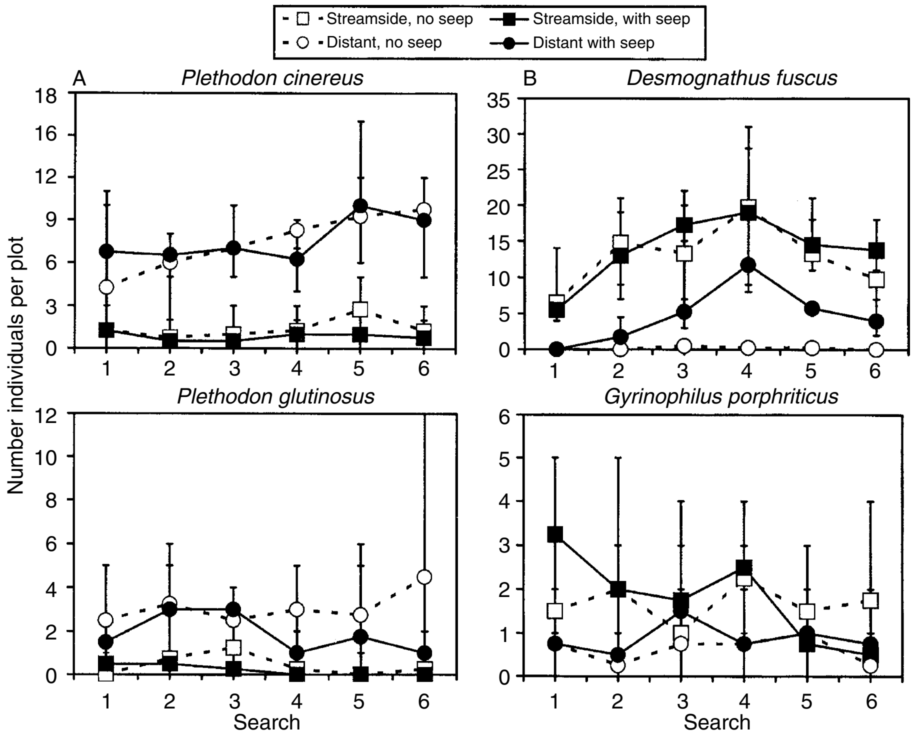

*Figure 5-23*. Effects of habitat manipulation in four species of salamanders by providing artificial seeper. Search has been repeated six time: Seepes were dismantled one month before the fifth search. The sixth search was conducted 8 months after the cessation of water flow from seeps (from Grover & Wilbur 2002, with permission).

the seeding of other plants. For instance, *Typha* spp. and *Phragmites communis* have the capacity to dominate in marshlands for a long time, like *Nardus stricta* in the mountain prairies. Some alien plants such as *Helianthus tuberosus* invade the river bed, creating dense monospecific covers preventing the settlement of native vegetation such as poplars, adlers and willows.

Some plants have the capacity to capture sediment transported by the superficial water or by the wind. These sediments, transformed by microbial processes, affect the cycle of many nutrients.

Grazing, breeding and digging and seed predation are the main activities of animals in ecotones (Figure 5.24). For instance, the cutting of trees by beaver creates ecotones composed of shrubs (Johnston & Naiman 1987). The snow vole (*Microtus nivalis*) especially in winter, eats blueberry plants (*Vaccinium* spp.) affecting the structure and diversity of grassland communities (Farina et al. 1986). Moles and ants modify the cover of upland prairies by soil digging and/or

*Figure 5-24*. The digging activity of the wild boar *(Sus scrofa)* creates new ecotones in the upland grassland along the Mediterranean mountain range. The grass cover is broken and new plants can avoid the strict grass competition.

the accumulation of vegetal debris at the nests. Termites modify the soil chemistry and feral horses modify the vegetation by grazing and the micro-topography by trampling.

Although internal factors are important for creating and structuring ecotones, often external events are fundamental to shaping ecotones.

For instance, an ecotone created by a fire largely depends on the frequency of this disturbance, but fires are conditioned by regional climates. The same may be observed for pH changes due to moss colonization. But moss colonization is determined by hydrological processes and microclimates that favor moss settlement. Internal factors are consequently subordinated to external factors in ecotone creation, structuring and dynamics.

## 5.3.10 Characters of the ecotones

### *5.3.10.1 Permeability of ecotones and diffusion of vectors*

The permeability of ecotones is the capacity to deflect the movement of a vector; it is an inherent character of the edges and is species-specific, when animal vectors are considered (Wiens et al. 1985, Manson et al. 1999).

An ecotone has a different permeability according to the strength of the vector, such as wind or water, to cross and to transport, and the transported material has more probability to be captured in the ecotone patch when the kinetic fall is higher.

In animals, the greater a species' body mass, more permeable the ecotone (Wiens et al. 1985). The physiological attitude may be important to consider how more or less permeable are ecotones. Species sensitive to microclimate gradients may recognize an ecotone as a barrier and species with defensive mechanisms can move more across ecotones than species with less defensive mechanisms. In a system dominated by edaphic components, the diffusion of water, energy and nutrients varies according to the texture, structure and organic content of the soil. The non-uniform distribution of these elements creates spatial gradients. The patch edges may be sharp, diffuse, linear or convoluted and can incorporate small or large patches (Stamp et al. 1987, Wiens 1992).

The flux of the organisms across the edges of the patches is regulated by abiotic, biotic, species-specific, and individual factors. The diffusion of an organism in a homogeneous environment is the same in all directions, but if a gradient such as light, salinity, humidity, structural complexity of the vegetation exists, then the diffusion is more directional (Figure 5.25).

All these factors may change among the different types of patches. Some differences can be perceived by animals such as birds, which can be attracted by the higher diversity and complexity of the vegetation. In fact, at the edges, there are more possibilities for nesting and better food availability. Also, the predation may be higher, in this case, edges can be true ecological traps.

The presence of borders should have an effect on species dispersal according to the level of perception of the focal species. For instance, Matthysen

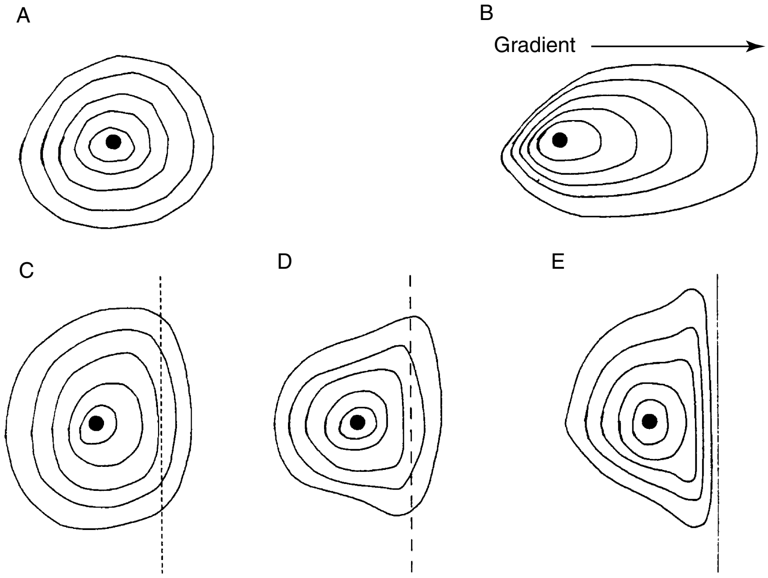

*Figure 5-25.* Hypothetical behavior of material or organisms released from a central point (dot): in (A) a perfectly homogeneous environment, (B) along a gradient, (C) a system with a permeable bound, (D) a system with a semipermeable bound, (E) a system with an impermeable bound (from Wiens 1992 ,with permission).

(2003) found in great tits (*Parus major*) a significant tendency to emigrate in the direction of the nearest patch border but not for Blue tits (*P. caeruleus*).

Ecotones are important not only for the movement of the species but also for the energy and resources moved by species such as ants, which move material from one patch to another. Beavers modify the hydrological flux, by creating temporary dams and this produces changes in many ecosystem cycles (Johnston & Naiman, 1987).

The topography affects the dimensions of the fluxes due to the kinetic energy and the ratio surface/volume of the water masses. The high ratio surface/volume of the dam created by beavers increases the changes at the borders and the reduction of kinetic energy due to the dam effect increases the sedimentary capacity of the particles (Johnston & Naiman, 1987).

When the contrast between neighboring patches is very high, the edges become true barriers. Human activity has favored these conditions that are more rare in nature. As true membranes, the edges can be permeable to some fluxes, while they are impermeable to others. The edges between the different components of a landscape are, consequently, very important for the properties of all the systems.

For instance, wetland ecotones have been found as refuges for endangered fishes in Lake Nabugabo, after the introduction of Nile perch (*Lates niloticus*) as reported by Chapman et al. (1996).

As with animals, plants are sensitive to the presence and characters of edges. Sarlov Herlin & Fry (2000) have studied the distribution of woody vegetation in forest edges and in hedgerows in 28 km$^2$ area of southern Swedish agricultural land. They found a significantly higher occurence of wind-dispersed species in forest edges, but in hedgerows, animal-dispersed species were dominant (Table 5.4). Hedgerows seem to be more attractive to animals that forest edges. The increasing width of forest edges and hedgerows was found to more positively affect animal-dispersed than wind-dispersed species. *Corylus avellana*, *Prunus padus* and *Viburnum opalus* were found more in hedgerows with a higher proportion of forest in the surrounding 500 m. This can be explained as a major attraction of higher proximity (physical connectedness) of forested area for seed-disperser animals. This study has clearly demonstrated (although indirectly) the strict relatioship between animal habits, landscape mosaic structure and plant adaptation, and offers important suggestions for landscape planning.

### 5.3.10.2 Animal movement across ecotones

Abiotic or biotic vectors actively move energy or materials across the system in a non-random way. For example, animals have a complicate behaviour when deciding to cross the ecotones (Martin et al. 2001). The permeability of an

*Table 5-4*. Dispersal mode, shade tolerance, frequency of occurence and $x^2$ test significance level between forest edges (n=262) and he edgerows (n=315), in a rural area of southern Sweden (from Sarlov Herlin & Fry, 2000, with permission).

| *Taxa* | *English name* | *Shade tolerance* | *Frequency of occurrence* | | | |
|---|---|---|---|---|---|---|
| | | | Forest edges | Hedgerows | $x^2$ *values* | *P-values* |
| Animal dispersed | | | | | df=1 | |
| *Corylus avellana* | hazel | 6 | 0.61 | 0.45 | 15.40 | *** |
| *Crataegus* spp. | hawthorn | 7 | 0.59 | 0.54 | 1.57 | N.S. |
| *Euonymus europaea* | spindle | 6 | 0.42 | 0.59 | 16.10 | *** |
| *Malus* spp. | apples | 7 | 0.14 | 0.17 | 1.49 | N.S. |
| *Prunus avium* | wild cherry | 4 | 0.18 | 0.49 | 60.40 | *** |
| *Prunus padus* | bird-cherry | 5 | 0.50 | 0.40 | 5.79 | * |
| *Prunus spinosa* | blackthorn | 7 | 0.42 | 0.54 | 9.21 | ** |
| *Quercus robur* | oak | 7 | 0.50 | 0.54 | 0.35 | N.S. |
| *Rosa* spp. | roses | 8 | 0.52 | 0.64 | 9.28 | ** |
| *Sambucus nigra* | elder | 7 | 0.61 | 0,58 | 0.64 | N.S. |
| *Sorbus aucuparia* | rowan | 6 | 0.14 | 0.27 | 15.80 | *** |
| *Viburnus opalus* | guelder-rose | 6 | 0.14 | 0.11 | 0.28 | N.S. |
| Wind dispersed | | | | | | |
| *Acer platanoides* | maple | 4 | 0.16 | 0.11 | 3.01 | N.S. |
| *Alnus glutinosa* | alder | 5 | 0.36 | .27 | 5.73 | * |
| *Betula pendula* | silverbirch | 7 | 0.11 | 0.09 | 1.04 | N.S. |
| *Carpinus betulus* | hornbeam | 4 | 0.23 | 0.08 | 27.90 | *** |
| *Fraxinus excelsior* | ash | 4 | 0.58 | 0.55 | 0.84 | N.S. |
| *Populus tremula* | aspen | 6 | 0.10 | 0.07 | 2.23 | N.S. |
| *Salix* spp. | willows | 7 | 0.12 | 0.32 | 32.60 | *** |
| *Tilia cordata* | lime | 5 | 0.08 | 0.03 | 6.38 | ** |
| *Ulmus glabra* | wychelm | 4 | 0.43 | 0.38 | 1.17 | N.S. |

ecotone depends both on active and passive diffusion in a species-specific way, by the perception and by the decision to cross (Wiens et al. 1985; Wiens 1992).

a. Passive diffusion (pd)

The rate of diffusion, the viscosity and heterogeneity of the patches are factors that affect passive diffusion using wind, water or biological vectors and may be represented as:

$$P(x1,x2)pd=\o(di, vj, hj)$$

where P(x1,x2)pd is the probability of passively moving from position x1 to position x2, di diffusion rate, vj patch viscosity j, hj patch heterogeneity j.

b. Active diffusion (ad)

This variable represents the capacity of an organism to move actively in the environment and depends on the rate and type of movement, density of organism in the patch, social interactions and habitat preferences.

$$P(x1,x2)at=\o(vj, hj) +\o(ri, pai, di, si, pri)$$

where P(x1,x2) at is the probability of movement from point x1 and point x2 of the organism i, ri-rate of movement of the organism i, pai-movement type, di-density of organisms, si-social interactions, pri-preferences for different environmental conditions or microhabitats in the patch.

The movement of an organism is influenced by the rate of movement and the shape of trails. Animals with high mobility move across longer distances when compared with sedentary species but this varies according to the season and site fidelity. The density of organisms in a patch is a very important factor, especially if there are social interactions.

c. Probability of edge encounter

The spatial arrangement of an ecotone, the shape and the size are important factors in the probability that an animal will meet an ecotone.

$$p(ek)=\{\o(aj,\ sj,\ poij)\} + \{p(xi,x2)\ pd+p\ (x1,x2)\ at\}$$

where: p(ek) is the probability to encounter an edge k , aj sj-area and shape of the patch J, poij-the instantaneous position of organism i in the patch j, p(xi,x2)pd-probability of passive diffusion, p(x1,x2) at active diffusion.

d. Probability to cross a boundary

When an organism is close to a boundary, three variables have to be considered: the species-specific permeability, the perception of the border; and the level of selection of the patch.

$$p(ck)=\o(permk,\ perki,\ selji)$$

where: p(ck) is the probability to cross an ecotone, permk is the permeability of the ecotone conditioned by two other variables permk = ø(sk,cok), sk is the sharpness or thickness of the boundary, cok is the contrast across the boundary between the neighboring patches; perki is the perception of boundary k of the organism i and selji is the selection of patch j.

e. Costs/benefits balance

The permanence of an organism in a patch depends on the balance between costs and benefits for patch occupancy.

$$selji= \o[(cj/bj)/(cm/bm)]$$

where: cj is the cost associated with the occupancy of patch j, bj are the benefits associated with the occupancy of patch j and the same for patch m.

The costs/benefit balance depends on many species-specific variables balance like the intra and inter-specific competition, the predation risk, physiological stress, resource availability, the cost of food searching and mating and the reproductive success.

$$cj/bj= \o(comj,\ predj,\ psj,\ resj,\ forj,\ mj,\ reproj)$$

where comj-intra and interspecific competition, predj-predation risk, psj-physiological stress, resj-resource availability, forj-foraging cost, mji-mating success reproj-reproductive output.

### 5.3.11 The function of ecotones in the landscape

Ecotones represent semi-permeable membranes across the landscape and modify the direction, the type and the dimension of material and information exchanged with the neighboring systems (Forman & Moore 1992; Yin & Lan 1995). For example, Peterjohn & Correll (1984) have found that in a small catchment, the riverine ecotone can incorporate the surplus nutrients flowing from the surrounding fields.

Ecotones have been described at several scales, have been found in many environments and play an active and passive role in energy and nutrient fluxes. Less known is the role that they have in the maintenance of landscape stability and the way in which resilience and the resistance are transmitted to the adjacent systems (Baudry 1984; Forman 1981; Merriam 1984). For instance, a riparian woodland increases the stability of the neighboring fields by reducing the effects of river flooding.

However, many species of insects harmful to agriculture find a favorable habitat in the edges, reducing the stability of the agro-ecosystem. Contemporarily, edges reduce the negative effect of wind by modifying temperature and soil moisture. Using adaptive plants, it should possible to improve the environment quality and optimize the resources. The importance of ecotones is emphasized especially in restoration ecology. Ecotones are easily manipulated if compared with other systems such as forests or grasslands.

### 5.3.12 The role of the ecotones in maintaining local, regional and global diversity

Along the edges, the abundance and diversity of animals are higher when compared with the adjacent habitats. This phenomena is known by wildlifers as the “edge effect”. Not all species have this response when in the ecotones but the extension and the quality of the ecotones are important to biodiversity. However, conversely, other effects can be observed at ecotones, like an increase of predation (Fenske-Crawford & Niemi 1997) and the loss lives of inner species (Kroodsma 1984).

Animals living in the ecotones such as amphibians, spend most their lives in terrestrial habitats but move to ponds to breed. Some species of birds such as finches spend the day in ecotones and roost in the forest. Many woodland birds during migration utilize these open ecotones as stopovers (Farina 1987, 1988). In many cases it is possible to predict the biodiversity according to the density of the ecotones.

Highest biodiversity is obtained when there is an optimal blend of patches and ecotones. When a landscape is characterized by large patches, the number and extension of ecotones is expected to be low. In this landscape, the biodiversity will be low. On the other hand, when the landscape is highly fragmented, the inner species will suffer (Figure 5.26).

When ecotones are considered as linear habitats, like in the case of linear herbaceous elements, butterfly diversity has been found to be related to such elements by Ouin & Burel (2002) in hedegerow agricultural landscapes (Figure 5.27).

In urban areas, ecotones have been found to maintain a higher number of true forest plants and species groups of high conservation value by Godefroid & Koedman (2003) and these findings can be utilized in order to manage forest plants in urban contexts.

## 5.3.13 Human impact on the functioning of ecotones

Inner and outer edges are common both to natural and to man-made landscapes. Some of these edges are easily localized, like the edges between fields and woodlands, or between one type of vegetation and another (Figure 5.28). Others, as such ecotones at different salinity or pH, are difficult to perceive without tools.

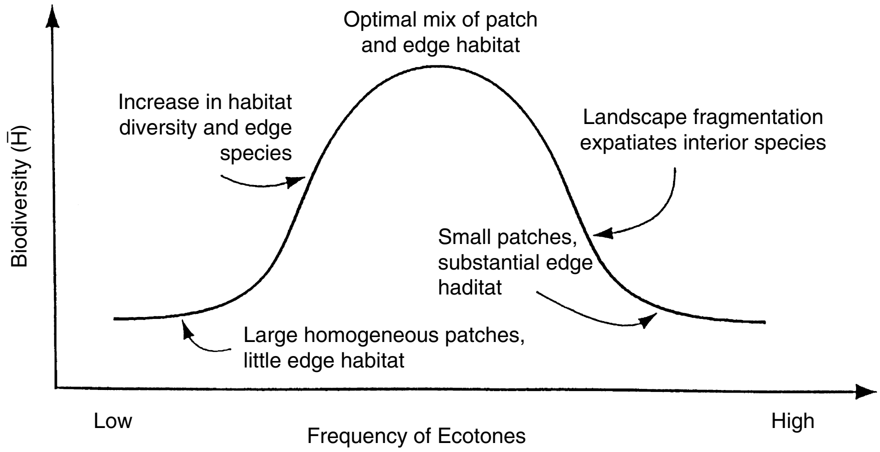

*Figure 5-26*. Frequency of ecotones and biodiversity value (from Naiman et al. 1988, with permission).

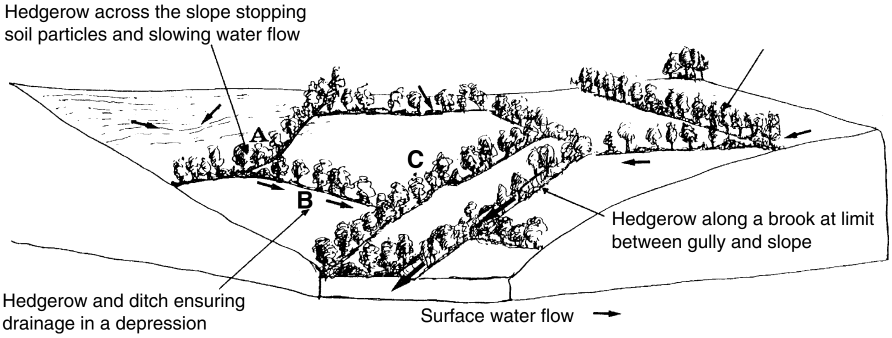

*Figure 5-27*. Ecotones created in agricultural mosaic play a fundamental role in preventing erosion, improving microclimate, and adsorbing pollutants and nutrients (from Burel & Baudry 1990a, with permission).

## 5.3.14 Climatic changes and ecotones

There is much evidence that $CO_2$ produced by factories and by car circulation released into the atmosphere and contemporarily the reduction of tropical forests, are producing a climatic change in our planet. An international program of the ICSU (International Geosphere-Biosphere Program IGBP) was prepared in 1986 to study the physical and chemical processes that are at the basis of the functioning of the earth's system (DeFries & Malone 1989).

*Figure 5-28*. Ecotone at the tree line (Cavalbianco Mt, northern Apennines). The beech forest ends sharply at the mountain prairies. The extent of the structural ecotone is a few metres. Human influence is evident in shaping this landscape. A line of old trees was maintained as a border between the beech coppice and prairie.

In 1987, a report of the World Commission on Environment and Development of the UN (Brundtland 1987) increased the awareness of the scientific community to the consequences for the Earth.

Suggested for the first time by Griggs (1937), the utilization of the ecotone paradigm to appreciate the climatic changes has been recently reused by paleobotanists to study recent changes in vegetation cover (Delcourt & Delcourt 1987).

The organisms living in transition zones between two communities may be at the limit of their tolerance of local conditions and may then react very soon. With the increase in temperature, most of the soils will face drought. Many species will be able to readapt their eco-physiology but at a broad scale, changes in vegetation cover are expected.

At the biome ecotone, for example, a reduction of alfa diversity is expected.

The climatic changes do not have the same effect on all habitats. Some habitats have an intrinsic fragility such as the high mountain habitats. In this case, the climatic change will be more visible.

### 5.3.15 The economy and ecotones

The importance of ecotones has been recognized by humanity right from the prehistoric period. The first villages and cities were situated on ecotones such as lake and sea coasts, or in the river delta (Desaigues 1990).

The economic evaluation of ecotones in man-made and modified systems seems vey important. The suppression of many ecotones such as lagoons and marshes apparently represents an economic advantage because they make available new soil for cultivations and urban development, but at long temporal scale they represents a net cost for the disequilibrium and breaking of water and nutrient cycles at the landscape level. The productivity and the functionality of a system are assured by ecotones. It is the case with riparian woodlands that represent buffer zones, reducing the eutrophication of fresh water (Peterjohn & Correll 1984) and functions as a good barrier to catastrophic water flash flooding.

Humanity has received many benefits from ecotones. In this way, the edges separating fields have been built up to reduce the wind effect, changing the microclimate of the soil and favoring plants and animals. However, all these man-made ecotones are fragile structures.

The recent intensification of agriculture has produced the disappearance of edges from large parts of rural European areas (Burel & Baudry 1990a,b).

Ecotones like marshes and river deltas and estuaries have been considered expensive to reclaim and, on the other hand, the recent discovery of the invaluable role of these areas for maintaining biodiversity represents two faces of the same coin.

Using a long-term perspective, ecotones represent important areas to maintain a balanced mosaic and sanctuaries for many species of plants and animals.

## 5.3.16 Genotones

The concept of ecotones can be extended to the spatial arrangement of genes in a population. A good example is the distribution of three genotypes of *Drosophila pseudoobscura* along an east-west transect in the southern areas of south-west of the United States (Dobzhansky et al. 1977) (Figure 5.29).

In particular, we call the change of a species character along a geographic range cline. Recently, Schilthuizen (2000) revisited the theme of ecotones as zones in which parapatric speciation is active. The idea that an ecotone could be an active zone where new species evolve is gaining the attention of many

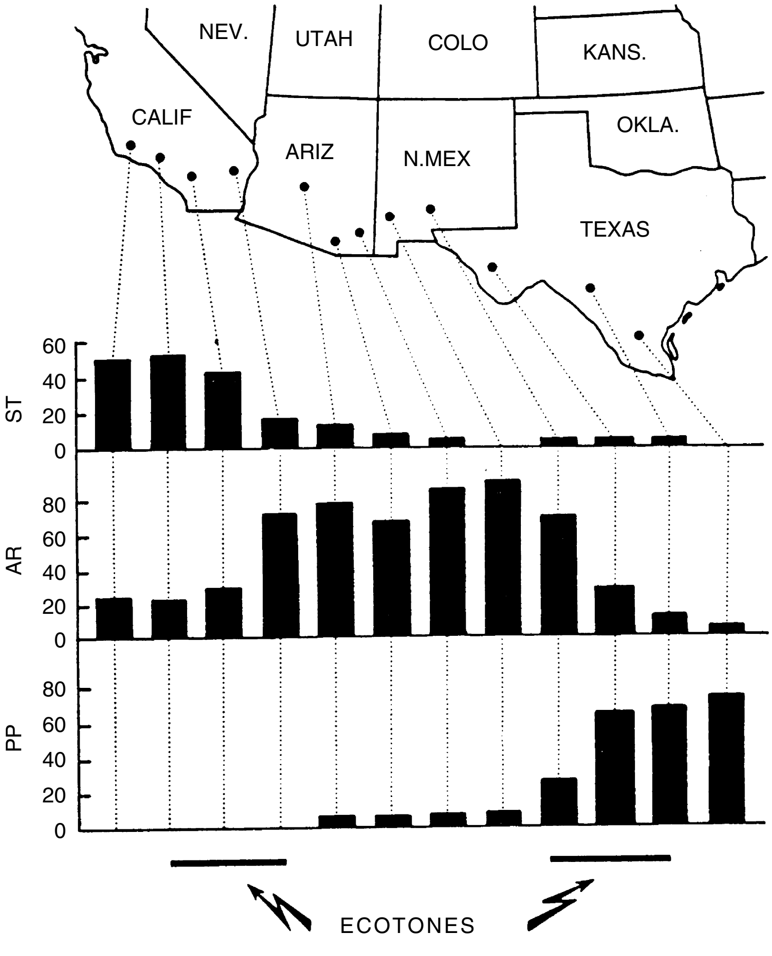

*Figure 5-29.* Frequency of the spatial distribution in third chromosomes of *Drosophila pseudoobscura* in the southwestern United States. The genotones can be localized where the gradients in chromosome frequencies are steep (from Dobzhansky et al. 1977, with permission).

researchers. For instance, Schneider et al. (1999) have tested the hypothesis that parapatric speciation could be active in a population of *Carlia rubrigularis* a leaf-litter skink of the Australia tropics. This species occurs in the closed rainforest as well as in open eucalyptus forests. The ecotone between these two habitats is no larger than a few hundred meters. Perpendicular to this ecotone lies the Black Mountain Corridor (BMC), a known biogeographic barrier of the pre-Pleistocene period. Despite a morphological difference between the two populations living on the two sides of the ecotone, these authors found a strong gene flow across the ecotone. Along the BMC was found a high divergence in gene sequences but not a morphological differentiation. Despite the strong gene flow, the environmental gradient (at the local scale) has effected a morphological divergence. Further research is necessary to better investigate the role of ecotones in speciation but promises exist for attracting ecologists and geneticists at the boundaries.

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# Chapter 6

# PRINCIPLES OF LANDSCAPE DYNAMICS

## 6.1 INTRODUCTION

The land mosaic generally does not have a permanent shape but changes as size, shape, spatial arrangement and quality of the patches. These dynamics are the result of complex, multi-scalar processes, and have a tremendous importance for most living organisms (Brozovic et al. 1997) (Figure 6.1).

Changes occur either in the vegetation, animal population and also in cultural perceptions of the surroundings, in human intellectual activities, such as politics and economics (Merriam 1988). Changes occur also in the places and names (Sousa & Garcia-Murillo 2001). Among the several drivers responsible for landscape changes, policies occupy a high score in many regions like Europe, as argued by Fjellstad & Dramstad (1999).

Changes in landscape happen in very short time. Thirty years seems a sufficient period to accertain deep changes, especially in human-dominated land mosaics, although it is not easy to find any correspondence between statistics and landscape patterns, as argued by Van Eetvelde & Antrop (2004) in the traditional landscape of Southern France. Often, changes occur either in structure functioning and not all the elements of landscape are involved at the same time. Caution is requested in interpreting changes when a landscape is considered in its totality and integration between spatial (structural) and implicit (functional) data is recommended, as suggested by Lipsky (1995) for a key Czech rural landscape study.

Flows are the linking processes in the mosaic (Wiens 1995) and movements are related to flows. Movements are scaling processes and understanding processes requires a multiscale approach. For this purpose, fractal analysis

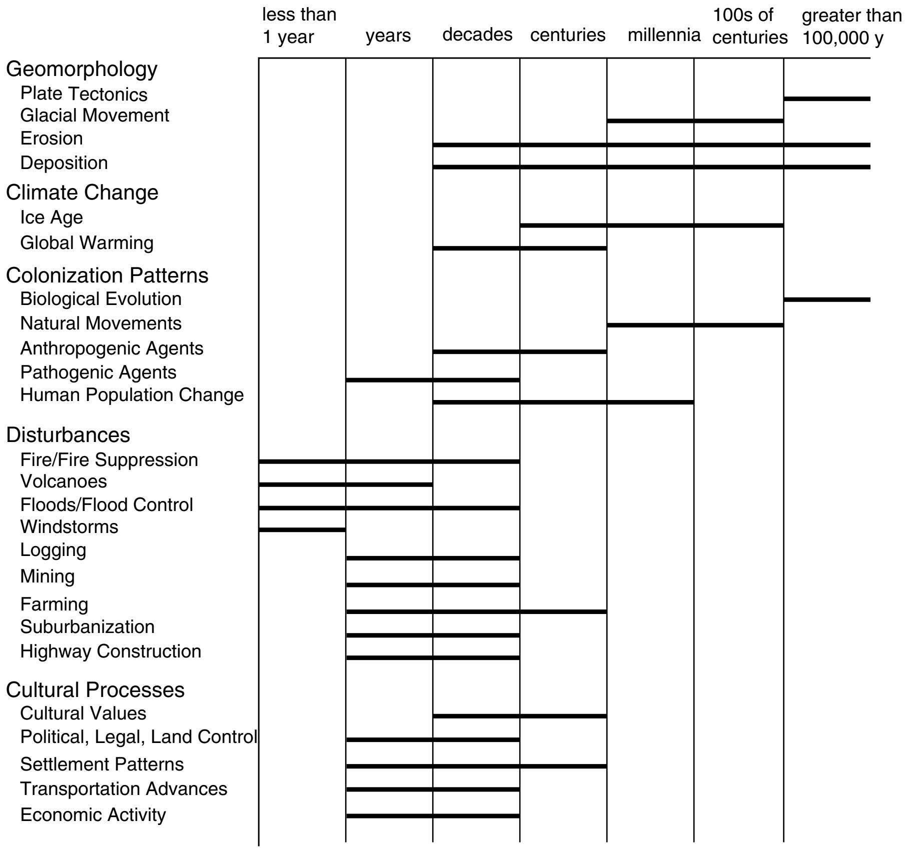

*Figure 6-1*. Time scale for relevant processes acting as drivers of landscape changes (from Marcucci 2000, with permission).

seems to be a very promising tool (Krummel et al. 1987, Milne 1991), as described in Chapter 8. The movements of energy, matter and organisms across a mosaic find constraint or gradients where a homogeneous patch meets a difference for some characters.

Today, many studies are available on the functioning of small-scale systems (ecosystemic approach) but little information is available when we approach large-scale systems and historical data are required (Axelsson et al. 2002). This fact largely depends on the relatively new scale adopted and, secondly, on the difficulties of integrating or combining at higher level the information of subordinate levels. Internal and external stimuli can produce changes in the system. Landscapes, like other natural systems, can exhibit different behavior when subjected to natural or human-induced stresses.

A system can react to these stimuli by resisting the external perturbation, which is measured by the degree to which a variable is changed from its equilibrium.

Ernoult et al. (2003) argue that the landscape reacts at least on two organization states, alfa and beta. The alfa organization measures the degree to which the distribution of selected features (land use) deviates from a random distribution. The beta organization measures the degree of deviation that one property is independent by the distribution of another.

The dynamics of a landscape depend at least on four major factors:
Disturbance frequency.
Rate of recovery from disturbance.
Size or spatial extent of the disturbance events.
Size or spatial extent of the landscapes.

Turner et al. (1993) have distinguished the temporal parameter (T) as defined by the ratio of the disturbance interval (i.e., the interval between successive disturbances) to the recovery time (the time required for a disturbed area to regain a "mature" stage.

Three cases are possible:

The disturbance interval is longer that the recovery time (T>1).
The disturbance interval is equal to the recovery time (T=1).
The disturbance interval is shorter than the recovery time (T<1).

And the spatial parameter (S) defined as the ratio between the size of disturbance and the size of the landscape of interest. There are two types of spatial ratio.

The disturbance is larger then the landscape of interest, in this case the landscape dynamics can not be predicted because the landscape is too small to characterize the effect and recovery from the disturbance.

The disturbance is smaller than the extent of the landscape. Many landscapes can be affected by different disturbance regimes acting at different spatio-temporal scales.

Understanding the landscape dynamics has tremendous implications for landscape management and reserve planning. It is clear that the larger a reserve the higher the probability that a landscape can incorporate natural and man-made disturbances.

The scale-dependent nature of the concept of landscape equilibrium allows one to accept this concept only for a specific spatial and temporal scale.

The confirmation that the spatial setting of an ecosystem within a landscape influences many of the ecosystem's properties is of increasing importance and this can be well demonstrated, especially when data are available from long-term studies (Kratz et al. 1991). However, it is not well understood, how a landscape influences the dynamics of a component ecosystem. There is little doubt that landscape influences are important to control ecosystem processes. For this, the application of the non-equilibrium concept to the study of an ecosystem seems very promising. It is clear that an ecosystem shows variability when an external stimulus (stress) such as acid rain or climatic change occurs. We can expect a low variability in ecosystems in which the landscape constraint is low, and *vice versa* high variability, when the position of the ecosystem in the landscape is more exposed to changes. For instance, on a mountain ridge, the weather conditions can change abruptly in a short time and we expect strong influences on the ecosystems that occupy this position.

But even in ecosystems that receive the same weather, we may expect that landscape position may be a predictor of temporal and spatial variability. For instance, geological processes such as erosion and deposition can cause land forms that have a deep influence on soil characteristics. These differences may have strong effects on biogeochemical processes, such as water retention, chemical buffering capacities and the dynamics of microbial communities.

From the study of Kratz et al. (1991), in which 68 parameters were measured, although the implicit limitation of a temporal grain size was of one year with an extent of 5 yr, it emerged that individual locations in each landscape differed from one other in their annual variability. At each site, the variability patterns of at least a subset of their parameters were associated with a particular subset of parameters, demonstrating that landscapes influence the temporal dynamics of ecosystems in a predictable way.

The factors that control soil cover heterogeneity can be produced by different constraints. In dry landscapes, the distribution of soil vegetation is not continuous but vegetation is patchily alternated with bare soil. Ludwig et al. (1999), investigating the processes that create in dry soils such alternation of patches and fetches at a fine scale (<5m), have found that contrary to expectation, the ratio between fetches and patches was not decreasing, thus decreasing rainfall in sands and loams. In effect, an increase in rainfall is positively correlated with the tree cover and this last character is negatively correlated with patch cover. In areas of savanna with a higher rainfall, trees control the size and spacing of ground-layer patches. But at the same time, a decrease in rainfall shifts the control of ground-layer patches to the runoff-runon processes as the major structuring processes of soil landscape. On clay soil this effect is not evident and the cover of patches was nearly 100% at the highest rainfall regime. Trees and shrubs were absent or had a low cover on clay sites. This example illustrates the complexity of landscape ontogenesis where concurrent agents (in this case soil and tree cover) are working.

### 6.1.1 The ontogenesis of the landscape (mosaic)

If we anaylze a landscape at the finest scale, most of the figures observed have a direct and strict relationship with the composing organisms (from bacteria to large mammals and plants). According to the cognitive paradigm, every organism perceives a species-specific landscape through bio-sensors and at the same time influence the specific surroundings (by trampling, browsing, shading, competeting). Several processes are influenced and manipulated by individual species, but we know that organisms are living in an environment (a higher-order organism system) and that such an entity is not only regulated by DNA coding or by teleonomic and autopoietic strategies.

The deterministic vision of the "microcosm" based on cause-effect cannot be used when moving to a higher hierarchical level, when we abandon individual species for bio/eco-systems. The landscape (mosaic) is an example of such higher-order organisms. Structure, patch composition and shape are not the result of individually-based choices but due to more complex interactions between genetic and stocastic processes. We must distinguish between our ignorance of the mechanisms and indeterminacy as an inherent property of these systems (Ulanowicz & Abarca-Arenas 1997). If the landscape, like the ecosystem, is not only the product of individually-based adaptation and related feedback, other mechanisms should also be invoked to explain the emerging order (*sensu* Stonier 1996). The organization of a system depends on the amount of information available into the system and by the energy that trasforms information into structural organization. That type of stochasticity operating in such conditions is easily demonstrated, but ignoring the mechanisms involved, we can use the frequency as an approximation and the scaled range of the processes in action. We have to abandon for a while the idealized natural processes based on specific adaptation and we try to analyze not the specific phenomenon but the generality of the process. We can reconstruct the complexity of our landscape (mosaic) under at least three main steps common to the majority of the observed landscapes that Farina (2004) calls respectively: opportunities, events and novelties. This vision is not far from the one presented by Fleissner & Hofkirchner (1996), which identified three different levels of system dynamics: micro, meso and macro-level. As you can see, the names of the steps are not peculiar but when we couple them to a specific meaning all these things gain the right position.

Opportunities (O), events (E) and novelties (N) differ in frequency (O-high, E-medium, N-low), in specific context (O-interior, E-intermediate, N-external) and in information refueling (O-intra-system, E-inter-system, N-eso-system), which means the manner in which energy enters and shapes the systems. The ontogenesis of the landscapes (mosaics) shows a recursive scalarity (O-E-N)-(Oi-Ei-Ni) and this means that each sequence can be found at a higher hierarchical level. Opportunities occur with the high frequency and shape of the interior patches or ecotopes producing coalescence in the composing communities. Events comprise the product of inter-patch (ecotope) contacts and create the ecotones (see later). Events modify the shape and exchange of matter, energy and information between patches, shaping the

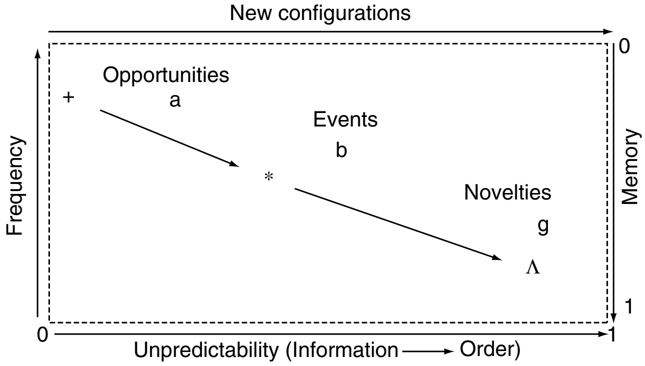

*Figure 6-2*. The three steps of landscape ontogenesis show different behaviors in terms of frequency, new configuration, memory and unpredictability.

(landscape) mosaic. Finally, novelties occur with the lowest ferquency and are activated by eso-energy that suddenly enters into a system, disturbing the spatial arrangement of a mosaic and creating new ones. Hurricanes are phenomena that introduce novelties into a system when they have enough energy. At the present time, when eso-energy (fossil and nuclear energy) is continuosly introduced into the system we expect an increase of novelty frequency that in turn can produce a more unstable configuration of the landscape (mosaic) (Figure 6.2).

## 6.2 STABILITY IN LANDSCAPES

We can consider stability as a family of processes having a capacity to reconfirm patterns and processes over time. The stability of a landscape could be an erroneous concept if used without a scaling perspective. We can expect stability across a range of spatial and temporal scales. In this way, the stability of a landscape has to be scaled according to the process that we intend to describe.

Generally, at a broad scale, changes of landscape structure and composition need a long period of time, but at a small scale, this can happen in a very short time. In natural landscapes, some structuring elements are more fragile than others. For instance, river vegetation is conditioned by seasonal flooding that can completely destroy the physical substrate on which plants were rooted. But in old growth forests, a severe fire could destroy some plants but not all the forest and this disturbance could easily be incorporated. A severe fire should be a rare event at a scale of hundred years.

The stability of a tropical forest is connected with the climate regime, by the rainfall. This stability may be reduced by rare events, such as large-scale hurricanes or by a change of atmospheric circulation due to jet stream currents. On the other hand, a riverain vegetation in the Mediterranean region is under a high-frequency threat of unexpected flooding and flashing that can dramatically change the shape and the structure of the substrate.

At the landscape scale, generally, stability is manifested by complicated patterns that locally present frequent changes but at a large scale they maintain the same shape. Thus, at the watershed scale, riparian vegetation appears more stable than when observed along a separate section of the river channel. This meta-stability represents a relevant character of every landscape.

Perturbations in stability occur in natural as in anthropogenic landscapes, producing apparently the same effects but caution has to be taken in terms of the functioning of the perturbed systems. For instance, human effects on the landscape vary according to the severity by which humanity changes the landscape and uses the resource. Hunting and gathering activity of the sparse primitive populations probably had scant consequences on the landscape structure. This effect could be compared with the effect of large mammals in African savannas if they are living in undisturbed condition without area restriction (Belsky 1995). In this case, the mammals are conditioned by topography, soil quality, energy and water availability. It is the landscape structure that drives the dynamics of the species, although locally, the ephemeral effects of trampling, grazing, urine and pellet deposition can produce disturbances.

When these conditions are menaced by area restriction due to human influence, the pressure of mammals on the landscape becomes the main shaping force, producing a different landscape in which patches of different quality are created according a differential pressure.

## 6.3 SELF-ORGANIZING MECHANISMS AND LANDSCAPES

A self-organizing (or self-reinforcing) system may be defined as a system in which structures and processes mutually reinforce each other (Wilson & King 1995). This system can maintain order through internal interactions and can be considered as anti-chaotic systems. Unlike a chaotic system, which is highly sensitive to original conditions, in this case the initial conditions are channeled into the same final state.

In ecosystems, there is a strong positive feedback among plant mutualists and heterotrophs. A complicated chain of interspecific interactions creates guilds that decrease the probability of the threshold of food chain collapse.

These interactive self-reinforcing communities are spatially integrated in a landscape whose dynamics are themselves self-reinforcing.

In some landscapes, disturbances are incorporated but in other cases they are magnified. In both cases there is a process of reinforcement of the structure. For instance, large stands of old-growth undisturbed forests are less susceptible to catastrophic fires are then acting to preserve forest structure. On the other hand, a fragmented landscape composed of young stands and a grass layer is more susceptible to catastrophic fires.

The Mediterranean landscape is a typical example of this last case. The landscape is highly susceptible to fires and most of the plants and their structures favor fire contagion.

## 6.4 LANDSCAPE SHAPING FACTORS

A hierarchy of factors shape a landscape. In general terms the first position is occupied by climatic conditions.

Recently, Bailey (1995) has described the ecoregions of the United States, basing the classifications on to Dominion, Division and Province.

Character of air masses is the first criteria, then intensity of radiation and, finally, seasonal changes in the climatic regimes.

Severe climatic conditions, like ice storms (Millward & Kraft 2004), may produce a different impact on the landscape according to local topography (elevation and aspect), forest composition (deciduous or coniferous) and the metereological characteristics of the disturbance (Figure 6.3).

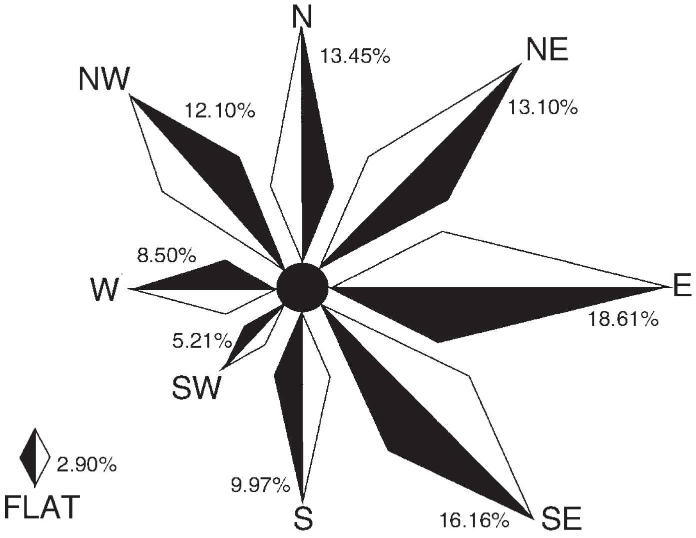

*Figure 6-3*. Percentage of damaged forest canopy by a severe ice storm in northeastern North America in 1998 as functions of aspect (from Millward & Kraft 2004, with permission).

Soil is modified and deeply influenced by climates and then vegetation criterion. Vegetation has some capacity to modify soil but causes and effects are difficult to separate. Animals represent the last step in this rank but there can be many exceptions such as in the semiarid regions in which termite activity can change the functioning of vegetation.

## 6.5 LANDSCAPE CHANGES IN HUMAN PERTURBED LANDSCAPES

Landscapes can present changes due to many different natural and human-induced perturbation regimes. Undoubtedly, human intervention on the natural arena has been dramatic during the last two centuries, and the role of history in shaping landscapes is the central part of landscape ecological evaluation (Antrop 1997) (Figure 6.4). Natural perturbations like flooding, wildfires and thunderstorms have a deep influence on the historical evolution of landscapes, but generally, human influence surpasses or masks these natural processes due to higher frequency of occurrence.

Relevant landscape changing processes related directly to human use are:

Agriculture intensification
Agriculture abandonment

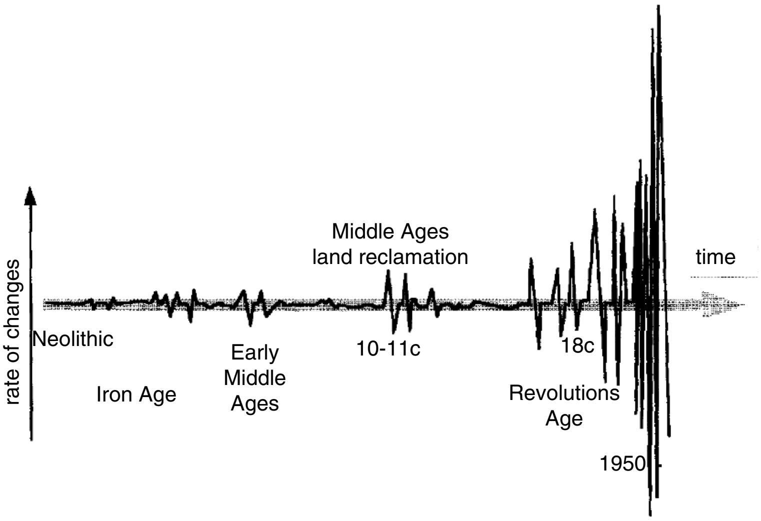

*Figure 6-4*. Conceptual representation of the frequency and magnitude of human-induced landscape changes in Europe (from Antrop 1997, with permission).

Fire suppression
Fire prescribing
Deforestation
Afforestation
Forest regeneration
Livestock grazing
Development

### 6.5.1 Agriculture intensification

This process generally produces a decrease in landscape mosaic complexity, a simplification of many geo-chemical cycles, a reduction of many ecological processes, a simplification in trophic chain and a decrease of system resilience.

Monoculture, created by a modern agriculture, is an extremely simplified system in which a considerable input of fertilizers allows farmers to maintain a high rate of harvests.

In this type of landscape, the linear features are dominant and generally, most of the soil is dramatically perturbed by seasonal plowing.

However, the negative effects of agriculture intensification have been found to be reduced as a result of contemporary afforestation, as argued by Vanacker et al. (2003), in a tropical mountain range of Equador. This mitigation has been explained by the contemporary afforestation of degraded lands with eucalyptus, which improves nutrients and soil water retention. Although this example can be validated only locally, the strategy to compensate degraded areas with afforestation in intensively farmed agricultural soil seems to work well.

Recent changes in agricultural landscape in western France have produced a decline in small mammals (rodents and shrews). In particular, small mammals have been found to be more sensitive to agricultural intensification than to the type of crop (Millan de la Pena et al.2003a), but also to changes in many groups of animals like spiders, carabids and plants (Burel & Baudry 1995, Millan de la Pena et al. 2003b) (Figure 6.5).

Agricultural effects on spontaneous vegetation mosaics in many cases present intriguing patterns. For instance, Great Plains grasslands are an endagered biome in North America because of agricultural activity that fragments and reduces native plant cover. The risk of reduction is a double effect of agricultural fragmentation coupled with juniperus encroachement (Coppedge et al. 2001). These authors, studying the land cover change in the period 1965–1995, have observed that juniperus expansion severely affects the survival of grassland communities more than cropland management, increasing grassland fragmentation initiated by human use of the land some centuries ago.

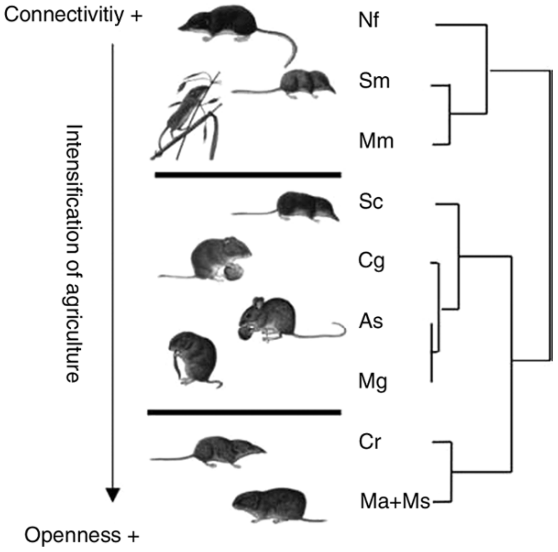

*Figure 6-5*. Effect of agricultural intensification on the assemblage of small mammals as the result of an analysis of barn owl (*Tyto alba*) pellets. *Neomys fodiens* (NF), *Suncus minutus* (SM), *Micromys minutus* (Mm), *Suncus coronatus* (Sc), *Clethrionomys glareolus* (Cg), *Apodemus sylvaticus* (As), *Microtus agrestis* (Mg), *Crocidura russula* (Cr), *Microtus arvalis* (Ma),) *Microtus subterraneus* (Ms) (from Millan de la Pena et al. 2003a, with permission).

## 6.5.2 Agriculture abandonment

Land abandonment is one of the more conspicuous phenomena in developed countries from Europe to North America (Figure 6.6).

The abandonment of agriculture is a pattern common to all industrialized countries, especially in hilly and mountain ranges. Well known across the Mediterranean basin, it is a relatively recent phenomenon in the last decades. We have dedicated more space to this process at the end of this chapter.

## 6.5.3 Fire suppression

Most natural and man-made landscapes have a patchy structure, which is important for many species of plants and animals. Especially in areas not heavily impacted by humans, fire represents the major driver of landscape perturbation. Fire suppression can deeply alter the dynamics and patterns of these areas.

After decades of fire suppression and the final recognition of the negative effect on landscape structure, fire prescribing has been utilized in different situations across North America. Cleland et al. (2004) have found that in

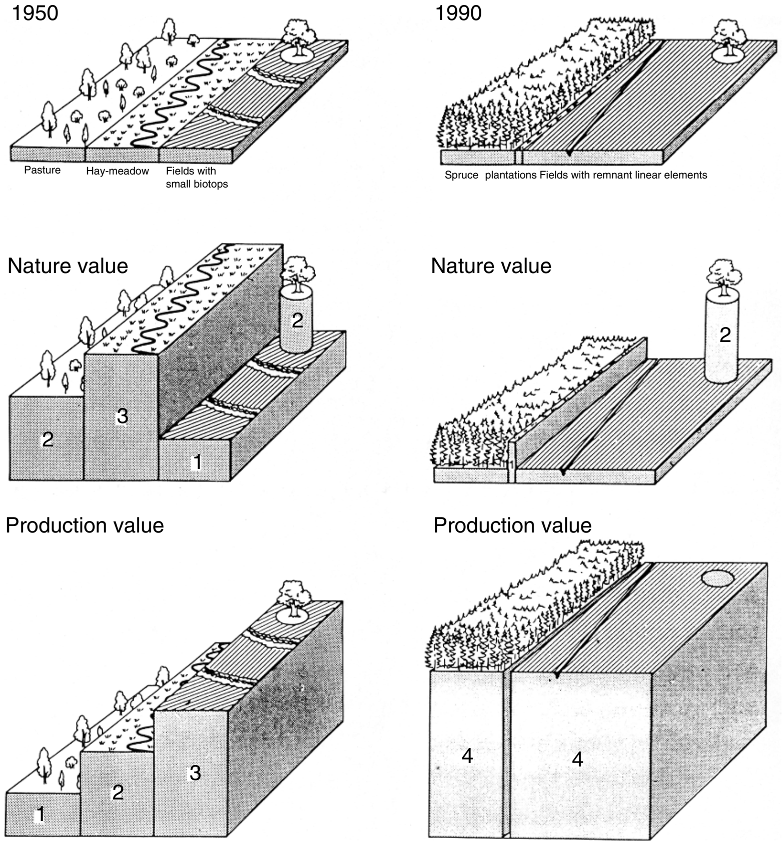

*Figure 6-6*. Changes in biological value and in production in a nordic landscape from 1950 to 1990. The land mosaic in 1950 was composed of pastures, hay-meadows and fields with hedgerows and scattered trees. In 1990, the mosaic is more simply, composed of spruce plantations and fields with thin linear hedgerows (from Ishe & Norderhaug 1996, with permission).

northern lower Michigan (USA), fire rotation increased from 250 years in the past to 3,000 years in the present. They argued that in the present time, land tenure in this region reduces the occurence of fire, thus depressing, the regulatory effects of fire on biomass and on community composition and coalescence.

Humans influence fire regimes with different consequences, according to the vegetation type. In San Diego County (California, USA) during the twentieth century Wells et al (2004) have noted an increase in fire occurrence in chaparral and in sage scrub, along with a decrease in hardwood and conifer forests. This demonstrates that fire ignition and the geographical location of vegetation are the variables to be considered. In densely populated low-elevation urban-wildland interfaces, fire occurence is higher. Forests are more effienciently protected by accidental fires.

When the fire regime in a forested landscape is suppressed, a cascade effect can be recognized.

Baker (1992) has used a model to study the effects of fire suppression, analyzing scenarios since the presettlement of Europeans in Boundary Canoe, Minnesota until the present.

For assessing landscape changes, this author used seven measures of landscape structure: mean patch size (total number of pixels of the study area/number of patches), mean shape s = (0.282 × perimeter)/area 0.5, mean fractal dimension (Krummel et al. 1987), Shannon index of diversity H = -Σpilog (pi) where pi is the proportion of landscape occupied by patches of age i, mean richness is the mean patch age, mean angular second moment is an index of fine-scale texture of the landscape (Haralick et al. 1973). He found that when the disturbance size and frequency decline for settlement and suppression, immediate changes occur in the landscape structure, as monitored by shape, Shannon diversity and richness. Some changes occur later (age, fractal dimension) or occur over hundreds of years (size, angular second moment).

When the disturbance regime is changed from presettlement to settlement, some measures react immediately (age, shape, Shannon diversity, richness, second angular moment) but others effects are not visible (size, fractal dimensions).

## 6.5.4 Deforestation

Despite an increase in the use of new plastic, metallic and "virtual" materials, deforestation is a conspicuous phenomenon in many parts of the world, especially in boreal and tropical forests.

Deforestation modifies the structure and functions of the landscape, increases fragmentation and thus the amount of edge habitats, increases the diversity of stand age, creates linear borders and facilitates the immigration of open space species into forest interiors.

We have to distinguish between the deforestation of primeval forests (tropical and boreal) that generally has severe consequences from coppicing in temperate forests. In this case, the logging is periodic and the perturbation regime is incorporated by woodlands.

In primeval boreal forests, the spatial arrangement of the logged stands have a tremendous importance in maintaining the biodiversity. Franklin & Forman (1987) propose a spatial model based on a checkerboard shape (Figure 6.7) in which the cuttings are dispersed as evenly as possible.

The landscape is strongly affected by the choice of forest exploitation patterns. The probability of disturbance (e.g., wildfire, windthrow and

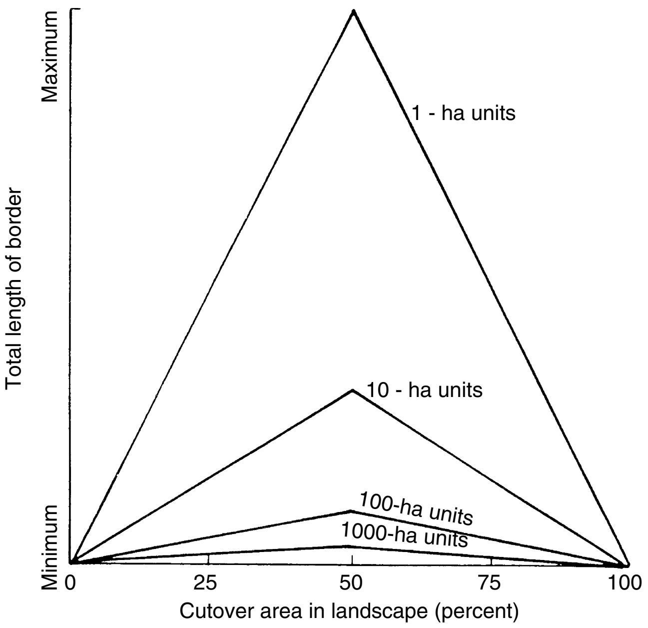

*Figure 6-7*. Total length of edge between forest and cutover area across different cutting-unit sizes (from Franklin & Forman 1987, with permission).

species diversity) are strongly sensitive to the spatial arrangement of the land mosaic.

Hayes et al. (2002), analyzing the change in forest cover in Guatemala's Maya Biosphere Reserve, have emphasized the relationship between road access and forest clearing, during an investigation of the last 23-year time period but this effect has recently been reduced by deeper farmer exploitation inside the forest. This is indirect evidence that socio-economic constraints can produce unpredictable modifications in human behavior that are apparently less ecological balanced (Figure 6.8).

White & Mladenoff (1994) studied the evolution of a 9600-ha landscape in Northern Wisconsin from 1860 until the present. The forest composition from pre-settlement to post-settlement changed from a landscape dominated by *Tsuga canadensis* to hardwood forest (*Acer saccharum, Betula alleghaniensis*). From 1860 to 1931, large disturbance processes associated with logging were dominant. After 1931 the dominant process ensured an increase of homogenization in the landscape.

In forest landscapes, changes in land cover can be observed using a very short temporal scale. Wolter & White (2002) have used a 5-year interval to evaluate changes in northeast Minnesota.

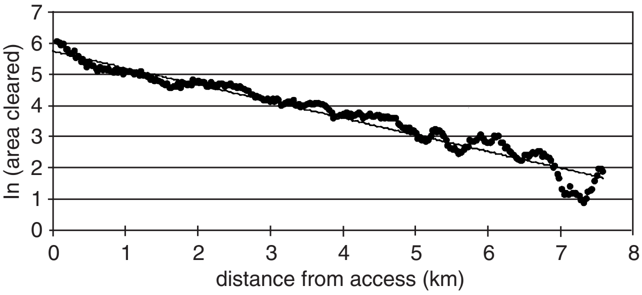

*Figure 6-8*. The relationship between cleared areas (in log scale) and the distance from access by roads and rivers in Guatenala's Maya Biosphere Reserve (from Hayes et al. 2002, with permission).

McGarigal et al. (2001) have discussed the cumulative effect of roads and logging across the mountain landscape in the San Juan Mountains (Colorado, USA). Half of the mature coniferous forest was converted during the period 1950–1993 to young stands, mean patch size and core areas have been reduced by 40% and 25%, respectively. Roads increased three-fold. The cumulative impact of logging intensification and road increase is apparently negligible if a scale of 10-year periods is adopted, but assumes a dramatic character over a 40-year period. Finally, if a large spatial scale is adopted (228,000 ha) the change in landscape structure is trivial. This means that landscape at the regional scale has the capacity to incorporate such disturbances. However, if an intermediate scale (1,000–10,000 ha) is adopted, a change in landscape mosaic is quite evident. This evidence must force ecologists and planners to select the scale of evalutation to describe changes that affect landscape health more efficiently.

### 6.5.5 Livestock grazing

Many regions of the world are interested in the spread of grazing disturbance regimes by livestock. The effects on the structure and functioning of landscapes are dramatic. Domestic grazers create landscape patterns with a different environmental impact according to the conditions in which they are reared.

This disturbance is density dependent and plant adaptation to grazing is strictly linked to the severity of the disturbance. Often, when the density of grazers is high, other effects are added, such as trampling and increasing of the soil nitrogen.

Landscapes react promptly to grazing regimes, modifying the plant community. Under a moderate grazing regime, the plant diversity is enhanced but when the grazing pressure increases, a quick drop in diversity is experienced in the plant cover.

Often, as in most of the US Western grasslands, the modifications of plant mosaic have been so severe that shrubby steppes have replaced annual and perennial grasslands.

With different the extensions and entities of mountain prairies across Europe, they have experienced grazing pressure for many centuries that has deeply modified composition and spatial arrangement of vegetation patch types.

### 6.5.6 Development

Urbanization and infrastructures like roads, railways and airports cover broad surfaces of the earth. The consequences on the landscape are intuitively extremely dramatic. Covering soils and destroying natural vegetation are added to the modification of surface and underground hydrological nets.

With the increase of urban areas, we expect a reduction of ecosystem services and a decrease of ecosystemic self-regulating mechanisms. In an urban area, the niche construction is adopted by humans as a general rule (Day et al. 2003) and most eco-fields necessary for biological and cognitive functions are artificially (engineering) provided by unlimited energy use, reaching the maximum scores for efficiency and human agreement.

Jennings & Jarnaging (2002) have found an increase in stream flows due to an increase in impervious surfaces in the upper Accotink Creek subwatershed (near Annadala, Virginia,USA) (see Table 6.1) (Figure 6.9).

A developed area is a tremendous sink area, demanding and adsorbing an enormous quantity of energy (from water to oil and food) and is a source of degraded energy (heat), wasted water and solid cabbages.

The increase of population around the world and urbanization in many regions are creating conditions for larger developed areas like Mexico City and Los Angeles. In Beijing, for instance, the urban area has been expanded from 269 to 901 km$^2$ from 1975 to 1997, with an increase of 2.35 fold in 22 years (Qi et al. 2004) (Figure 6.10). In these areas, the landscape is completely modified and natural patterns and processes are replaced by "artificial" structures. Core areas increase the relationships with the periphery and a strict relationship is

*Table 6-1.* Changes in demographic and farming variables in a region of Portugal (from Moreira et al. 2001a, with permission).

| *Variable* | *Period* | *% Change* |
|---|---|---|
| Number of farms | 1954–1989 | –33.6 |
| Number of cattle | 1954–1989 | –74.4 |
| Number of sheep | 1954–1989 | –93.7 |
| Number of goats | 1954–1989 | –95.3 |
| Population size | 1950–1991 | –31.3 |
| Number of farmers | 1950–1991 | –58.6 |

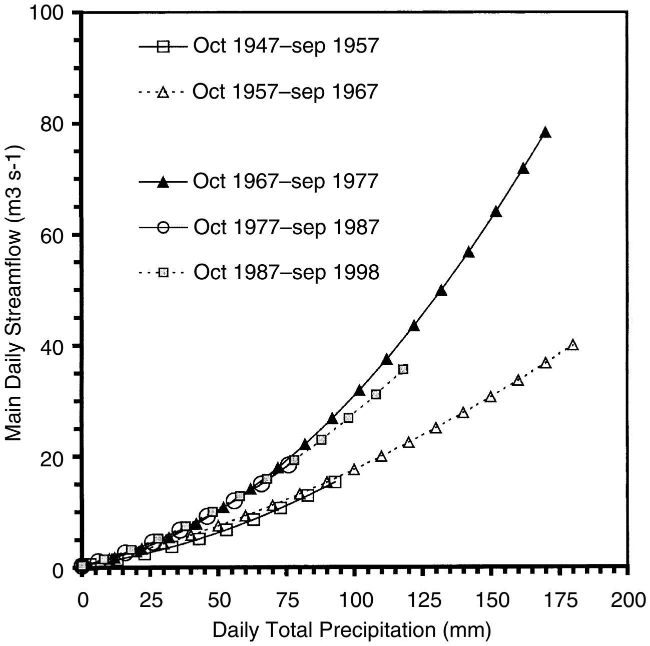

*Figure 6-9*. Changes in the response of daily streamflow to daily total precipitation during the period 1947-1998 along a decade-by-decade series of regression, in the upper Accontink Creek subwatershed (near Anannadala, Virginia, USA) (from Jennings & Jarnaging 2002, with permission).

established between the two. The capacity of the landscape to incorporate the disturbance is reduced or erased. For instance, if an entire watershed is occupied by developments, the functioning of this watershed will always be pathological. In this way, human strategy should be to mimic the natural processes, but often this is prevented by high costs, lack of information and knowledge and soil demand for infrastructures.

In the Phoenix metropolitan area, Luck & Wu (2002) have applied a gradient analysis and landscape metric and demonstrated that urbanization has consequences on ecosystems structures like density. In such conditions the center and spatial patterns of urbanization can be detected using a landscape approach.

The maintenance of forest islands inside the cities provides not only ecosystem services like amenities and recreation but can also provide a refuge to biodiversity. From a comparative study of beetle assemblages (Coleoptera, Carabidae) across the urban-rural gradient of Bulgaria, Canada and Finland, it appears that this group of invertebrate maintains a diverse structure when forest patches are preserved inside an urban range (Niemela et al. 2002).

## 6.6 PATTERNS IN LANDSCAPE CHANGES: SOME EXAMPLES

Natural and anthropogenic landscapes can be characterized by a different degree of fragility; in other words, according to their capacity to change after a disturbance. The interception of fluxes is fundamental for many processes and a knowledge of the spatial arrangement of the phenomena is critical to better understand the functioning of the systems.

Unfortunately, landscape changes are not easily detected on a short time scale and to investigate these changes necessitates field information of high quality across a long time lag which is not always available ( Petit & Lambin 2002).

In human-dominated landscapes, the variables involved in the changes are many and mostly strictly related to socio-economic processes (Figure 6.10). For instance, Fukamachi et al. (2001) have compared the use of resources and socio-economic elements as an indicator of landscape changes in an analysis from 1900 to the present. The more dramatic changes occurred from 1950 onwards. This seems to be a general trend around developed countries (Figure 6.11).

The uniqueness of landscapes prevents standard approaches in the study of environmental changes. This often depends on the information available, microclimatic and topographic characters, socio-economic history and trends.

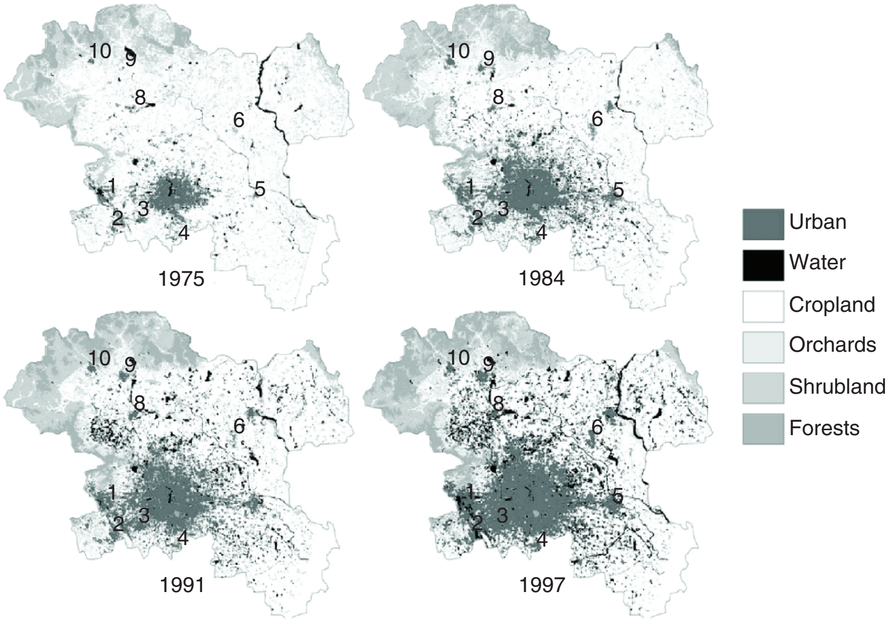

*Figure 6-10*. Increase of developed area in Beijing from 1975 to 1997. Land use and land cover were classified by using Landsat MSS and TM data (from Qi et al. 2004, with permission).

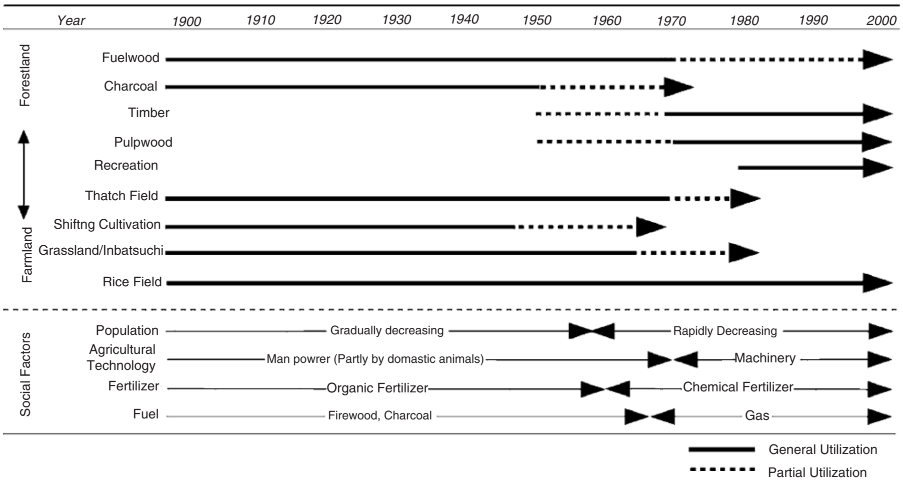

*Figure 6-11.* Changes in socio-economic and natural domains in Kamiseya, Kyoto Prefecture, Japan (from Fukamachi et al. 2001, with permission).

Simpson et al. (1994) have investigated the landscape changes occurring from 1900 to 1988 in two contiguous Ohio landscapes: a till plain landscape and a moraine landscape. This last landscape has a greater geomorphological diversity and heterogeneity.

Using aerial photographs from 1940, 1957, 1971 and 1988, combined with historical archives, the landscape information was transferred to a GIS for comparison. A different evolution was detected in moraine and till plains. On moraines, agriculture decreased as forest, urban and suburban areas and industrial settlement increased. In the till plain, agriculture increased until 1988. Land cover diversity and evenness were higher in moraine than in till plains at all dates. Moraine landscapes showed more dynamism while till plains showed more inertia. Factors that influenced the evolution of these landscapes are topography and soil capability, but also the socio-economic environment, like agriculture policies and patterns of urbanization. Socio-economic factors have to be coupled to physical and biological factors to understand the dynamics of human-perturbed landscapes.

Skinner (1995), using aerial photographs of a forested watershed of 24,600 Ha in north-western California, has compared the spatial structure of vegetation 41 years apart. In this area, a fire suppression policy has modified the dynamics of disturbance and the spatial arrangement of the patches. Fifty random sample points were selected in two 1:16,000 aerial photographs: one from 1944 and one from 1985. At each sample point it was calculated: (a) distance from sample point to the edge of the nearest opening; (b) distance from the edge of the first opening to the next, closest opening; (c) perimeter of each opening; (d) area of opening; and (e) the non-open area around each opening closer than any other non-opening. Opening perimeter was regressed against opening area. Other shape indices were utilized.The comparison between 1944 and 1985 openings resulted in reduced as expected under the fire suppression regime. The distance between openings increased significantly from 1944 to 1985. In conclusion, fire suppression has considerably changed the forest landscape in 41 years, but there were no significant differences in form or shape of openings.

Changes in landscape composition and their relationship with physiographic regions were evaluated by Turner & Ruscher (1988) in Georgia, US in a time lag of 50 yrs (1930–1980). Land use patterns were measured by mean number and size of patches; fractal dimension of patches; edge length between land use; index of diversity, dominance and contagion (see methods).

The results show a clear change in landscape according to the different physiographic regions (lower coastal plain, upper coastal plain, piedmont, mountains).

The Georgia landscape exhibited the greatest changes in piedmont. In general, the landscape appears less fragmented at present. The complexity of the patches decreased as shown in Figure 6.12 using the fractal index. These changes had a great effect on fauna, favoring forest species and affecting edge species. The landscape changes occurring in the last 160 years have been quantified by Iverson (1988) across Illinois State. Eleven soil attributes were used in the analysis. Naturally derived land types are closely influenced by landscape attributes (44 to 83% of variance). However, urban types, strip mines and quarries and reforested lands are not associated with landscape attributes (17 to 30%). This study clearly demonstrates the importance of landscape scale in evaluating land changes.

Changes in land uses and within a specific use like agriculture enable the observation of changes in the use of spontaneous resources. For instance, Slotte (2001) has documented the decrease of leaf-hay collection from deciduous forests due to feeding livestock (sheep and goats) in Swedish landscapes during the last two centuries and an intensification of arable lands (Figures. 6.13, 6.14).

Often, the interactions between different stressors like fire, grazing and climate change determine the landscape physiognomy. In the Wind Cave National Park, South Dakota, which represents a climatic ecotone between forest and grasslands, Bachelet et al. (2000) have found from historical records an expansion of forest after fire suppression. On the other hand, overgrazing by livestock has reduced the fuel load, facilitating forest expansion. In the past, when native herbivores were present in the area with lower density than the actual domestic grazers, biomass reduction was not so high as to reduce the fuel load that ultimately controls forest expansion and shrub encroachement.

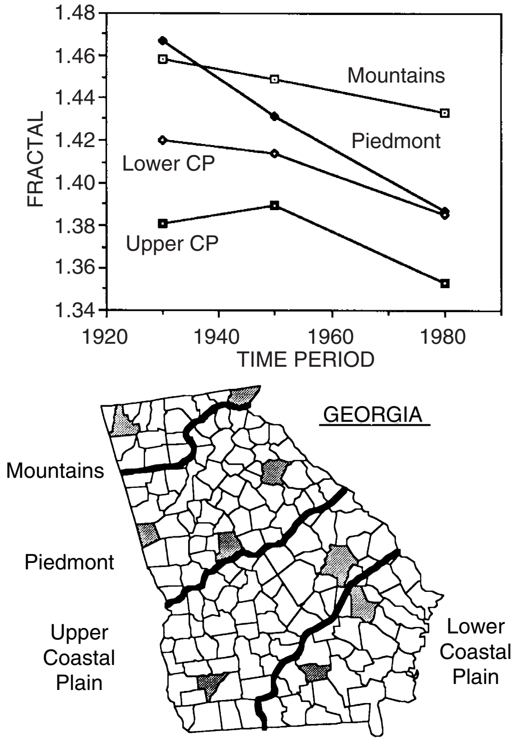

*Figure 6-12*. (A) Map of Georgia (counties) and physiographic regions (B) Fractal dimensions of patches in each physiographic region using all types of land uses (from Turner & Ruscher 1988, with permission).

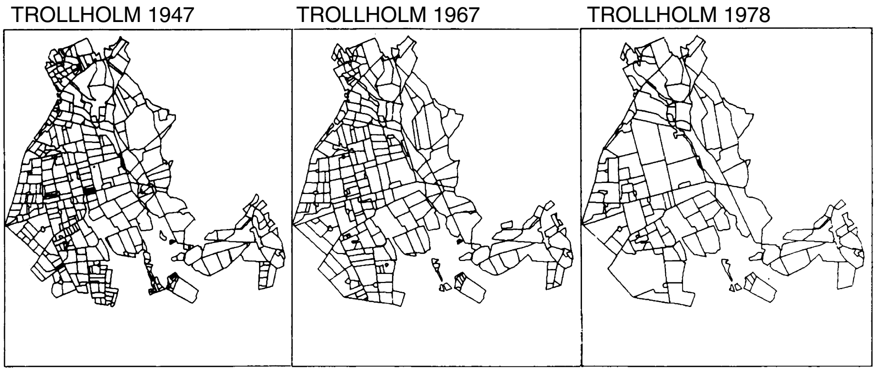

*Figure 6-13*. Example of cadastrial simplification in Trollholm estate in 1947, 1967 and 1978 (from Ihse 2004, with permission).

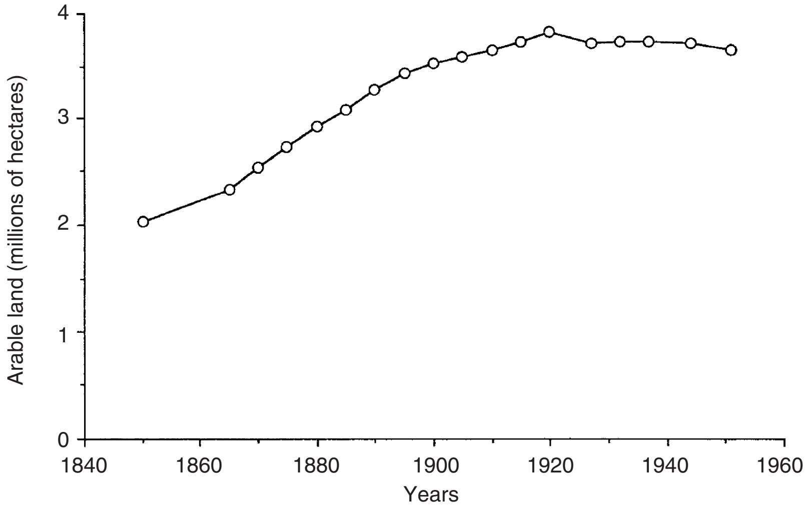

*Figure 6-14*. Arable land and twig leaves harvested in Sweden from 1850 to 1950 (from Slotte 2001, with permission).

## 6.7 MEDITERRANEAN LANDSCAPES AS AN EXAMPLE OF PERTURBATION-DEPENDENT HOMEORETHIC SYSTEMS

The Mediterranean landscapes have been extensively modified by an anthropogenic disturbance regime for thousands of years (Blondel & Aronson 1999, Grove & Rackham 2001). Local ecologically-related activities of crop raising and livestock management at a larger scale have been overlapped, time after time, by the intrusion of alien cultures during westbound migrations (Naveh & Vernet 1991).

We have scant information on the effects of these combined factors but we can imagine some destructive effects of a local metastability reached by a fine grained interaction of residents and their surrounding landscape. Some models from an alien culture, such as the Roman "centuriazione" (Caravello & Giacomin 1993) seems very successful, for instance, in the Po Valley (Northern Italy), persisting to the present time.

The roughness of the topography and the seasonality of weather events and life cycles have contributed to distinct microsite ecotopes.

The Roman empire deeply affected the communication among different people and for many centuries the circulation of items, seeds and animals has been encouraged. This has probably played a relevant role at the local scale compared to the input of new species after the discovery of the American continent.

The high ecodiversity of the Mediterranean region has been enhanced by a fine grained use of the resources in time and space. This probably has assured an "historical" sustainability for the populations although catastrophic events as drought, flooding, famine, wars and diseases have cyclically perturbated the system to a greater extent.

The fragility of the Mediterranean landscapes is connected to the human stewardship but resilient mechanisms have been adopted by plants, animals and systems. Logging, grazing and fire are the main sources of disturbance in the Mediterranean. The logging activity, mainly for charcoal and timbering, has been moderate thanks to the use of concrete to build houses. Grazing has been very strong in most of mountain ranges across the Mediterranean and, in many cases, overgrazing has exposed the soil to erosive processes, especially in the dry Mediterranean.

Fire has played a fundamental role in controlling open spaces in the Mediterranean. In fact, the maintenance of spaces have been a priority for the rural population in any time from the protohistoric period when hunting and gathering activities were dominant.

The fire tolerance of most of the Mediterranean plants, well demonstrated by may authors, have probably created most of the actual plant associations (Naveh 1990). Fire events affect soil erodibility differently and according to the pre-fire cover (see Figure 6.15). Fire severity affects diversity in vegetation

*Figure 6-15*. In the Mediterranean when fuel accumulation is high and the season is hot and dry, fires are often so severe to completely destroy the plant biomass and also devasting the superficial root system (Luscignano, Massa Carrara province Italy: summer 2004).

regeneration. As argued by Giovannini et al. (2001) intense fires may reduce the soil heterogeneity from past land uses (Figure 6.16).

The capacity of plants to react to seasonal stresses such as drought and fire is extraordinary across the Mediterranean. Bulbs, grow for a short period and abundant seeding using abiotic vectors such as wind and water and biotic vectors, like animal fur, are some of these escaping strategies.

But if these adaptations have been extensively studied by ethno-botanists and zoologists, an unexplored chapter is represented by the ecological adaptation of the systems to this disturbance regime.

In fact, it appears relevant that in the Mediterranean region, the complexity of abiotic, biotic and human interactions have produced a tremendous ecological diversity.

The ecological diversity allows the resilience of the system, definitely the sustainability. The whole Mediterranean is menaced by seasonal human overcrowdedness (mass tourism), especially along the coasts. This coastal development has definitively destroyed most the land-marine interfaces. We have lost an essential buffer zone in which energy and matter meet. The demand for food, water and energy has forced other regions, often mountainous ranges, to work as source areas for the coastal sink.

Some strategies have been refined during this long period of human-nature interrelationship and some examples will be presented from different parts of the Mediterranean basin from which a large amount of data is available.

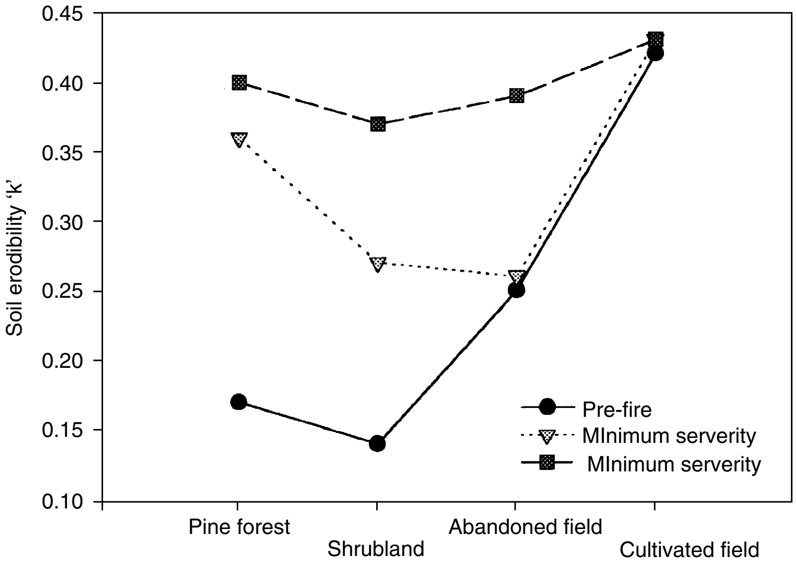

*Figure 6-16*. Soil erodibility estimated according the different land use in burned and unburned conditions across a dry Mediterranean region (from Giovannini et al. 2001, with permission).

From Portugal across Spain, footplain belts of oak savanna called, respectively, “Montado” and “Dehesa”, have been created by humans. This landscape is extremely characteristic and unique, similar to the African savannas (see Figure 6.17). Additional examples can be described such as the transhumance from mountain to lowland and *vice versa*. The seasonality of human use of Mediterranean resources is coupled with the seasonal phenology of many animals and plants. Geophytes escape the human disturbance (grass cut) reducing the living biomass to underground bulbs and many plants have benefited from sheep wool transportation of seeds.

In every light or severe human disturbance activity, plants and animals have the capacity to react. Secondary succession or mutualistic benefits are visible in every disturbance event. Human disturbance has for long produced definitive changes in the compositions of plant and animal communities; nevertheless, a diffuse biodiversity is still alive, also in overcrowded and used sites across the Mediterranean. Some plants have probably been induced to speciation by the urban habits of the older cities such as Athens and Rome (Celesti-Grapow 1995).

Animals and cultural landscapes have been particularly studied in recent years in the Apennines region (Italy) (Farina 1991, 1994, 1995). There is evidence that the open spaces of montane and submontane prairies and the terraced olive orchards and vineyard of *coltura mista* are preferred sites for many stop-over trans-African migratory birds and north-central Europe wintering birds (Farina 1986a). Favorable microsite temperature and abundance of food resources are important factors attracting the birds.

*Figure 6-17*. Steppic area in Alantejo (Southern Portugal). A relictual steppic zone maintained by human stewardship. In this area rare species like the great bustard (*Otis tarda*) (A) and little bustard (*Tetrax tetrax)* (B) survive. This is an example of nature-human interactions that allow to rare species to maintain stable populations.

Most of the managed lowland and marshlands along the Mediterranean coasts are key places for the breeding and/or the over wintering of many populations of wader birds. The Camargue and the Tuscan Maremma are the most famous sites, but from North Africa to Sardinia Island the coastal marshes are attracting many species of birds. The pastoral areas of uplands across the Mediterranean are important for the survival of wolves, bears and large scavenger birds.

The scenic value of these areas is strictly connected with high human-related ecological diversity, both ingredients for a human quality landscape.

Around the world, the cultural landscape has an additional value if compared with recently developed areas or with wild areas. In the future, more and more nature will be transformed by human activity and the challenge will consist in our capacity to mimic natural processes such as in the cultural landscapes, preserving fluxes of materials and energy.

Some basic ingredients of a cultural landscape are the survival and the healthy functioning of the basic processes. The fertility of the soil is maintained and restored after each harvesting by the input of livestock manure. The stream corridors and the edges are maintained in a healthy condition. This creates a gridding barrier against wind erosion, thermal excursion and frost exposition. Contemporarily edges are used by many ecotonal species and more tolerant plants and animals.

Birds have been studied largely in cultural landscapes (Farina 1986b; Purroy & Rodero 1986) and special attention has been devoted to the capacity especially for frugivorous species, to adapt to cultural landscapes. For instance, blackcap (*Sylvia atricapilla*) and song thrush (*Turdus philomelos*) have the capacity to track fruit availability in the olive ochards of southern Spain. These two species move from harvested to unharvested stands tracking fruit abundance and recognizing food abundance at different spatial and temporal scales.

Olive orchards are not homogenous plantations; composition density and ripping vary according to microsite quality, cultivar type and harvesting timing. Consequently, this landscape is extremely patchy and birds have the capacity to compensate fruit availability across the mosaic. This capacity has probably evolved in natural conditions before the human intrusion of the last millennia and this character has allowed many frugivorous birds to flourish in the Mediterranean cultural landscape. Birds have been found to be more abundant and the communities more diverse in rural areas than in woodlands in a sub-Mediterranean landscape of northern Italy (Farina 1997). More about the value of this landscape will be presented and discussed in the next sub-chapter.

The fact that traditional agricultural ranges across the Mediterranean are valuable habitat for many rare and endangered species is well documented and represents a concern for conservation biologists but also for policy makers (Delgado & Moreira 2000; Romero-Calcerrada & Perry 2004). Abandonment, agriculture intensification and urban and infrastructural development share the same responsibility for biodiversity depression as for soil erosion (f.i. Lasanta et al. 1995).

## 6.8 PATTERNS AND PROCESSES IN LAND ABANDONMENT

### 6.8.1 Introduction

Fragmentation and land abandonment are two main landscape processes that have modified a large part of our planet in a short time. Fragmentation (see Chapter 4) is produced by the removal of pristine or secondary forests to gain new space for agriculture.

Land abandonment, which has been extensively described in this chapter, is very common in industrialized countries (Baudry & Bunce 1991; Baudry 1991) and poses dramatic challenges to policy makers in terms of the conservation of natural, cultural and heritage capital (MacDonald et al. 2000) (Figure 6.18).

The great attention devoted to fragmentation is far from the modest attention paid to land abandonment. However, although it is common sense that fragmentation is producing a loss of biodiversity, the effect of land abandonment on biodiversity is not well understood and more in general the ecological diversity (see Olsson et al. 2000).

Probably, in some regions, this process is producing beneficial effects of biodiversity, especially if land abandonment occurs after intensive use of the land. However, in other regions than in the Mediterranean, land abandonment is producing not only a change in the biodiversity but a real decrease in the number of plants and animals. In this landscape, generally considered

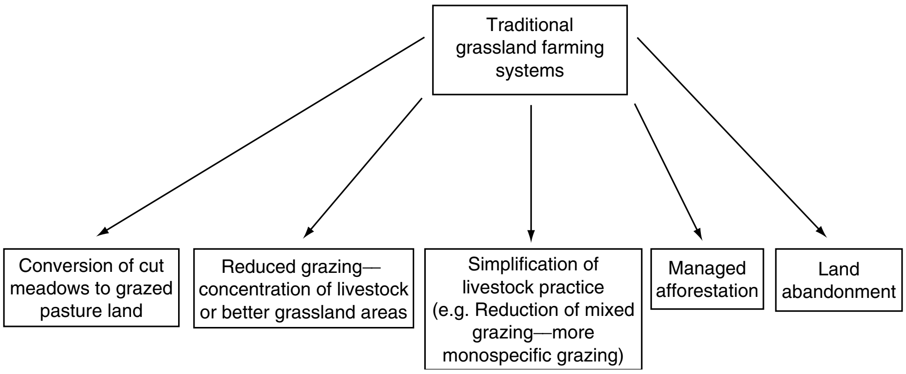

*Figure 6-18*. Dynamics of land abandonment according to two main European agricultural tenures (from MacDonald et val. 2000, with permission).

a cultural landscape (*sensu* UNESCO, see Chapter 7 for more details on the cultural landscapes) (von Droste et al. 1995), a fine-grained mosaic of fields and woodlots, a seasonal disturbance regime has maintained a great variety of plants and animals for thousand of years.

In this case, human stewardship has created a land mosaic extremely rich in local conditions. Human societies and the environment they occupy are closely connected; each social change coincides with a comparable change of landscape structure and functions. These modifications occur differently, according to the history of each country or group of countries but also for the climatic conditions. It is hard to draw any generalizations on these processes. In order to try to establish some rules for these complex phenomena we shall try to describe key cases on different continents, with a special emphasis on the Mediterranean region. It is not possible go come back in the time without the risk of handling too general information. However, before we commence with these considerations, we have to remove the dogmatic assumption that most terrestrial ecosystems have been influenced by humans only in the last centuries, without taking into consideration the more remote history of our ancestors.

Land abandonment is the most conspicuous process often associated with development. Generally, people move from uplands and bad land to lowlands and industrialized ranges.

The structure of the landscape and the effects on plants and animals are the most common issues (Burel & Baudry 1995). In particular across the Mediterranean, land abandonment, especially on mountain ranges, has been very common and widespread during the last 50 yrs (Farina 1991, 1994) (Figure 6.19) with consequences extending from trees to soil microbial assemblages ( Zeller et al. 2001).

Along the northern Apennines, land abandonment has been at a different pace and intensity according to elevation, topography and the local human community's history. Actually, the land abandonment has encouraged the woods to recover and most of the clearings were filled in a short time (Figs. 6.20, 6.21).

The uplands were important pastures for livestock, especially sheep. Actually, the pastoral activity has completely vanished and this grass cover is facing a quick change in vegetation composition.

One relevant consequence of land abandonment is the change in landscape mosaic due to woodland recovery. Generally, this process is not linear and in many cases it is interrupted by new disturbance regimes such as wild fires. In this case, although the vegetation is adapted to fire, when a fire event is repeated in a short time in the same place, the secondary succession produces an intriguing cover of weeds, parasitic and epiphitic plants. This condition is less favorable to maintaining a high level of biodiversity. Human-induced fires are probably a consequence of the loss of the economic value of the land. This hypothesis has been recently confirmed by observations on fire incidence in the

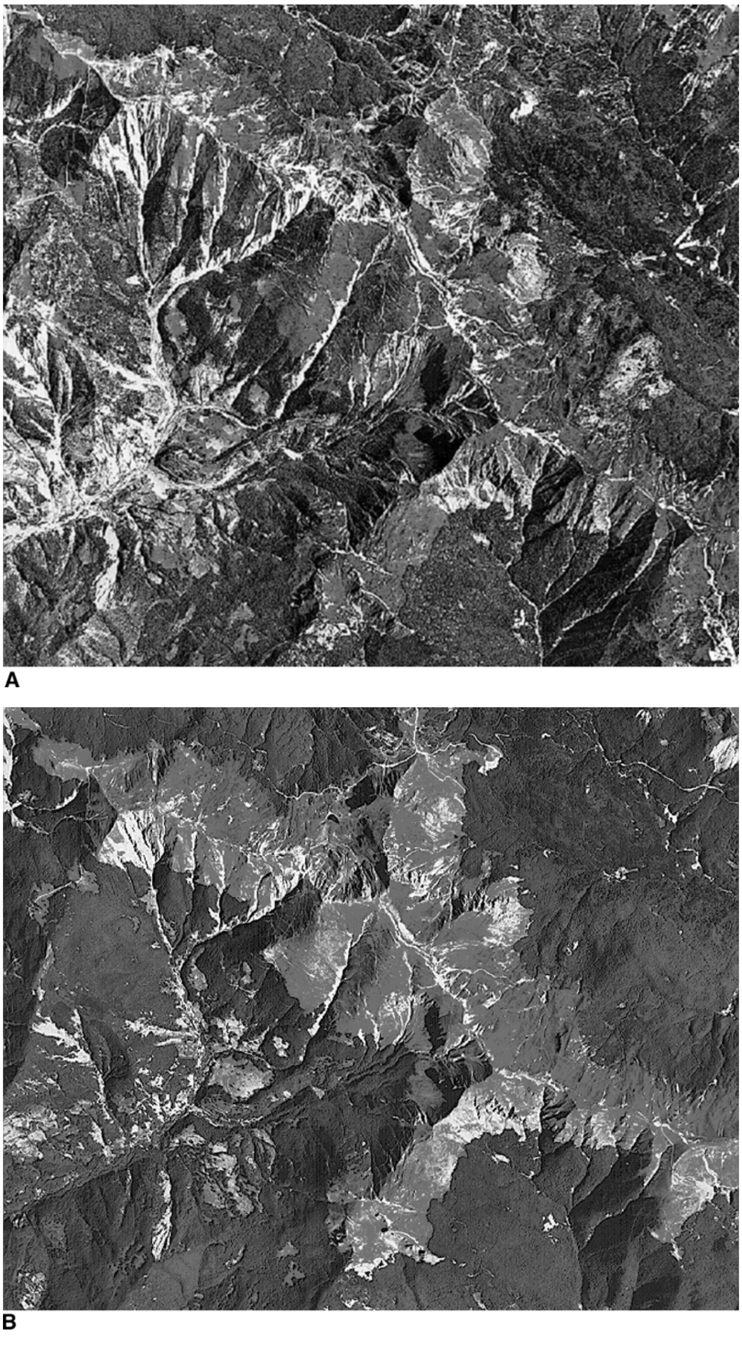

*Figure 6-19*. Effects of 50 yrs of land abandonment in a Northern Apennines ridge (Prado Mt, 2,000 m a.s.l.). (A) image of 1954. It is easy to appreciate the large amount of bare or thin grass layers and the topography relief. (B) The secondary succession occurred between 1954 to 1989 and has created dense beech forests and the regrowth of shrubs (*Myrtillus*) above the tree line (about 1500 m). Clearings in the beech forest have been filled in very rapid succession.

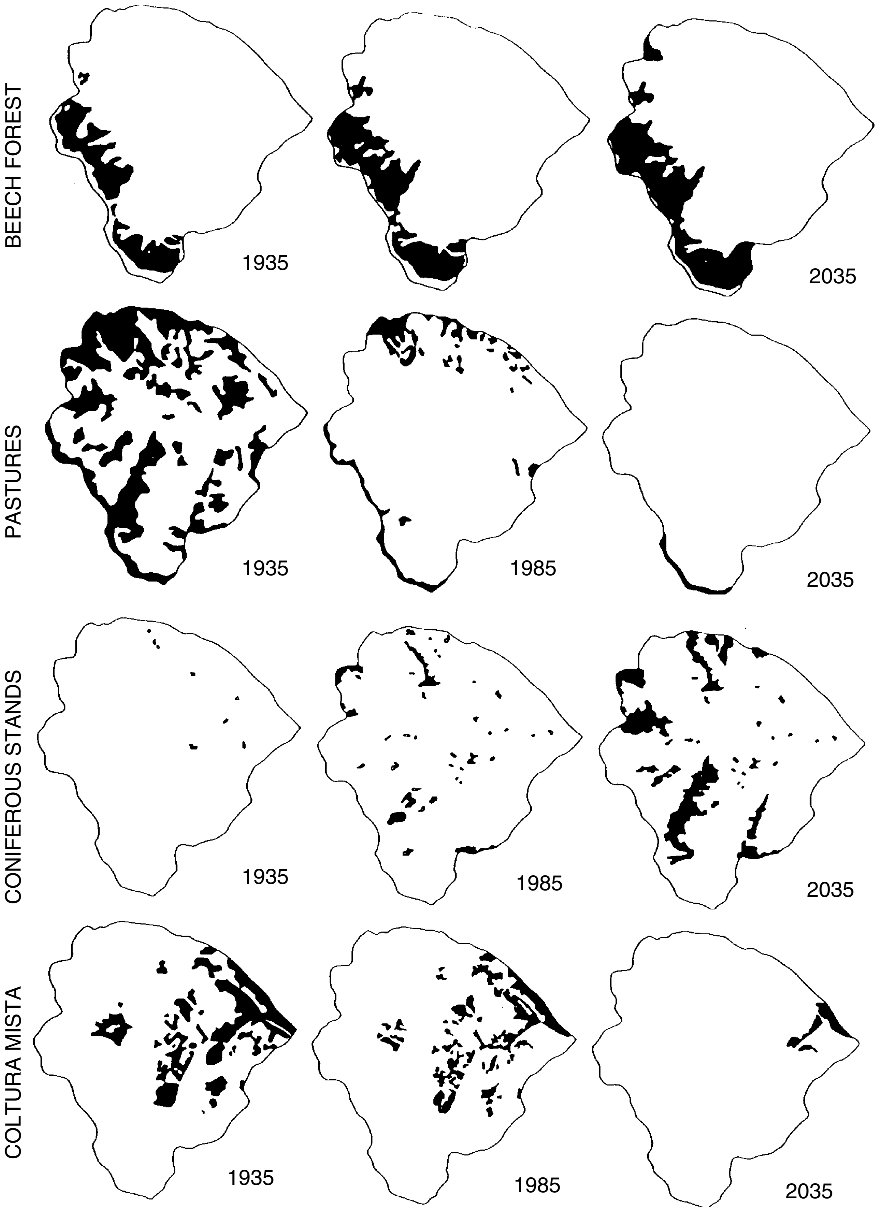

*Figure 6-20*. Effects of land abandonment in a Tuscan landscape (Solano basin) from 1939 to the 2035 prediction (from Vos & Stortelder 1992, with permission).

northern Apennines. Due to the oil crisis in the 1980s, wood for house heating was rediscovered as a cheaper resource. Coppicing practices, abandoned from more than 40 years, again started producing an immediate decrease in fire occurrences. This pattern has two distinct components; one component is

*Figure 6-21*. Effect of rural abandonment. The secondary succession develops in a short time forbs and shrub. In this image the terraced upland fields are invaded by ferns and *Juniperus communis,* and are moderately grazed (Camporaghena, northern Apennines, Italy).

linked to a changed human attitude toward the woodlands. The discovery of an economical value has probably created more concerns for fire. Secondly, the coppicing has created conditions less favorable to fire diffusion due to the presence of more forest roads and young "green" stands.

In Spain, many areas of traditional silvo-pastoral activity based on shifting agricultural systems combined with grazing, have quickly vanished, especially in less favorable soil. In the past, a long fallow period and the transformation of woodland into park-like savanna (dehesa) have been good strategies to reduce fire risk and assure a minimal biomass for livestock and modest yields from crops. The Dehesa assures biomass to livestock through the *Quercus ilex* leaves and fruit and from the legume-rich herb layer. Dehesa has a tree density of 40–100 trees per hectare. The land abandonment of Dehesa is producing a "matorralizacion" with the development of coarse grasses and shrubs more prone to fire risk. This decreases biodiversity as in other Mediterranean areas (Naveh 1974; Joffre et al. 1988; Gonzales Bernaldez 1991).

In the northern Mediterranean, the changes occuring in the landscape have been the direct consequences of the changes in social and economical models. After the second World War, dramatic social changes occurred in Italy and later in Spain and Portugal. Several analysis have documented the modification of the land mosaic. As reported by Moreira et al. (2001a,b) in Portugal, land abandonment has contributed to the increase of tall shrubland and woodland. This is evident from the demographic data (see Table 6.1), which emphasize depopulation in the agricultural regions and the disappearance of domestic animals like sheep and goats. One major consequence of such changes driven by the decline of agricultural activities is the increase of fuel accumulation and fires, along with an increase in the number and severity of fire events.

Especially in Portugal, montado changes pose noticeable problems for the future maintenance of such agro-silvo pastoral systems. In fact, as argued by Pinto-Correia & Mascarenhas (1999), it is not clear whether the current extensification of montado will lead to new equilibrium in an extensive silvo-pastoral or mere forestry system. Intensification and extensification often exist in the same property, creating a confused scenario. Uncertainty depends also on the possibility to manage large areas by using mechanization without producing degradations in soil and in vegetation cover.

Soil fragility is another important component to consider when changes occur in mountain terraced areas. In particular, Dunjo et al. (2003) warn that such types of soils can be degraded by runoff and nutrient loss.

### 6.8.2 The effects of land abandonment on fauna

The recovery of woodland and the loss of open spaces determine deep changes in animal assemblages in terms of abundance and species. In the Mediterranean, most of the relevant fauna is living in open spaces; their reduction produces local extinction, rarefaction and fragmentation of populations. The same process has been observed for forest fragmentation. Well-documented are the effects on the land mosaic (Vos & Stortelder 1992), birds and mammals (Farina 1994, 1995, 1997). The effects of land abandonment on bird populations have been investigated by Moreira et al. (2001a,b) in northwestern Portugal, arguing a primary role of fire for maintaining landscape heterogeneity and assuring a differential land cover.

In some transition phases, land abandonment creates a higher landscape heterogeneity but the succession moves so fast that in less than a decade grass layers are transformed into dense shrublands, a few of them are attractive to most of vertebrates and arthropods like butterflies.

While most open space birds are dramatically reduced by land abandonment (from partridge to stonechat) large mammals recover area, before hostile, and from which human competition had chased away (Apollonio 1996) (Figure 6.22). The spread of wild boar is a diffuse and common pattern in all southern Europe. This species, thanks to high adaptability to new situations added to a high fertility, became a true pest in many regions, with scant added of human control. The effect of this species on the environment is very high. Large flocks of wild boar can “plough” a prairie in a few hours or can seriously damage crops.

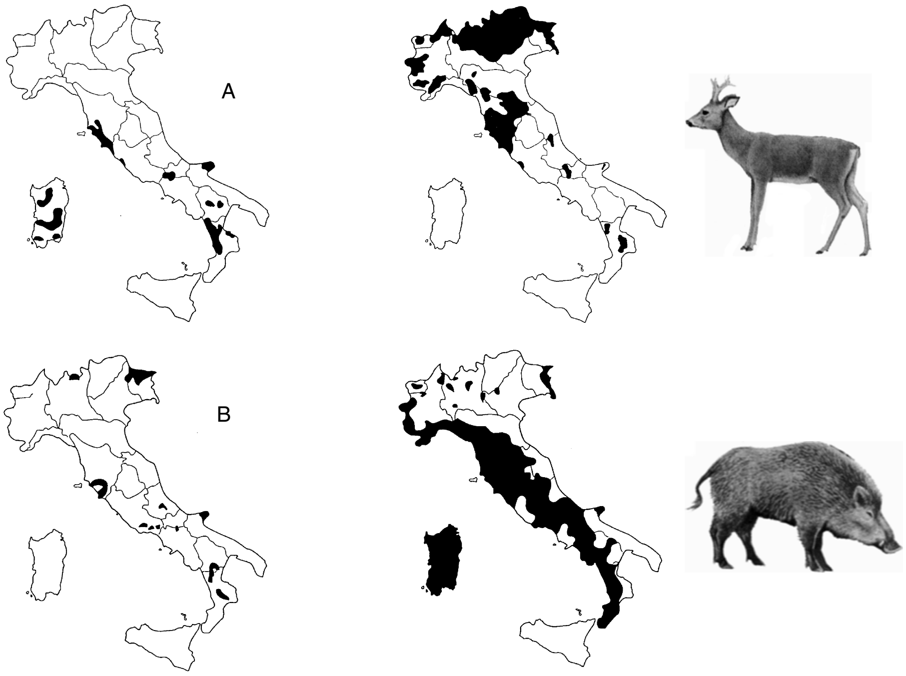

*Figure 6-22*. Distribution of roe deer (*Capreolus capreolus*) (A) and wild boar (*Sus scrofa*) (B) in 1911 and in 1987 in Italy. The diffusion of these mammals is strictly connected with land abandonment of hilly and mountain ranges (from Chigi (1911) and Perco (1987) quoted by Apollonio 1996).

The effect of digging on upland prairies is an open question for ecologists on the effects at medium and long periods on plant and animal communities. In fact, the change in disturbance has been dramatic for upland prairies. Only some decades before heavily grazed by goats and sheep and for few decades completely empty from any disturbance and then again, strongly disturbed by wild boar. Land abandonment has favoured roe-deer (*Capreolus capreolus*) across Europe. The presence of this species has been found to be a good (structural) indicator for vegetation type and landscape heterogeneity (Grossi et al. 1995).

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# Chapter 7

# PRINCIPLES FOR LANDSCAPE CONSERVATION, MANAGEMENT AND DESIGN

## 7.1 INTRODUCTION

Semi-natural, rural and agricultural landscapes, interdispersed urban centers and relevant infrastructures such as highways, bridges, dikes, electrical poles, etc., are widely distributed throughout the world.

The emergent characteristics of these landscapes are in synthesis with the fragmentation of natural remnant vegetation, high heterogeneity, interdispersion of different matrices of fields. Size, shape and spatial arrangement of the patches remain relevant for ecological processes.

The overlap of technological infrastructures (roads, bridges, railways) on natural structures like rivers, lakes, bottom valleys and ridges creates interference to many ecological processes such as soil erosion and deposition, water fluxes, animal movements and plant dispersion.

This chapter deals with the importance of landscape ecology as the scientific basis for the study, planning, and management of urban, semi-natural, rural and agricultural landscapes.

The capacity of the landscape ecology to track ecological processes across a range of spatial, temporal and cultural scales allows us to understand the real or potential effects of human land use and planning (Marcucci 2000; Wickham et al. 2000; Opdam et al. 2002; Alados et al. 2004; Hietel et al. 2004) of biodiversity processes (Cubizolle et al. 2003). An explicit application of landscape ecology principles to planning should permit mimicking and/or preserving natural processes more efficiently than using a non-spatial approach, as discussed by Forman & Collinge (1997). Its role seems as important in conservation strategies in pristine environments as in human-influenced landscapes (Jobin et al. 1995;

Reed et al. 1996; Santos Perez & Remmers 1997; Vos & Meekes 1999; Antrop 2000; Pirnat 2000; Bailey et al. 2002; Zechmeister et al 2003). Thus, in this chapter, our goal is to clarify the role of landscape ecology in the environmental issue which, due to a growing global deterioration of the biosphere, is of primary concern for ecologists but also for politicians and decision makers.

Landscape ecology can improve the anthropocentric approach to these issues in undisturbed and disturbed landscapes. The principles of landscape ecology can be utilized to plan or to manage key species, forest remnants, networks of edges and woodlots in croplands or to influence and redirect urban development (Clark & Slusher 2000; Rifell et al. 2003) and environmentally sensitive areas (Ndubisi et al. 1995). Special attention has been devoted to the value of "cultural landscapes" focusing on the importance of conserving the biological diversity and the diversity of many ecological processes to recognize the inherent ecological value of some man-shaped landscapes (von Haaren 2002). The importance of the cultural landscape forces us to pose this issue in the first place because most of the strategies that can be used to conserve pristine or deteriorate landscapes can find an immediate application in "cultural landscapes". Due to the broad spectrum of possibilities, we have reduced our presentation to exemplary key studies in an attempt to cover the more significant issues in nature conservation, management and planning (Figure 7.1).

## 7.2 LANDSCAPE EVALUATION

It seems a focal point in landscape management to assess the value of the landscape and to find criteria to evaluate the components. Naturalness has

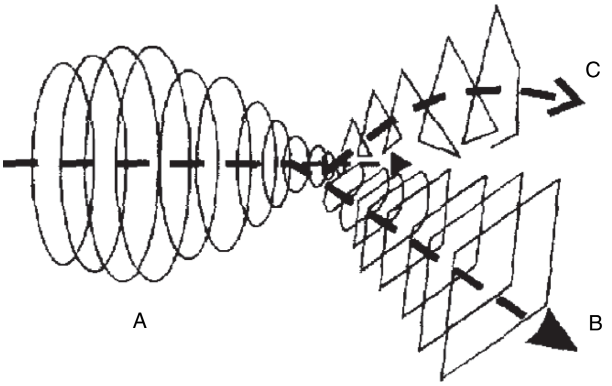

*Figure 7-1.* Conceptual model of the evolution of a traditional (cultural) landscape (A) into a "modern" landscape in which the planned landscape that tries to modify the existing landscape (B) can develop into an unexpected new system (C) (from Antrop 1997, with permission).

been proposed by Anderson (1991) as a conceptual framework, synonymous with intactness or integrity of ecosystems. This author proposed three indices of naturalness:

The degree to which a system would change if human interference was removed.

The amount of "cultural" energy required to maintain the functioning of the system as it currently exists.

The complement of native species that remains in an area compared with species present prior to settlement.

This concept is really popular because the word is attractive but it appears difficult to apply because often human exclusion from nature, depresses the biological and the ecological diversities. The general assumption that human influence on landscape is always negative should be removed. In fact, in some cases, human influence decreases the "value" of a site but in many cases it is necessary in order to maintain biodiversity (Gotzmark 1992). Most of the long-term human-modified landscapes can be considered "cultural landscapes". In these landscapes, human stewardship has created feedback with many ecological processes and the recreation of "natural landscape" appears more a suggestive dream than a scientific reality. At least half of the Holocene cultural landscapes were extended in a large part of Europe and in many other parts of our planet.

Landscape approach to land assessment can be successfully integrated with biological indexes like the Biotic integrity (IBI) and Habitat index (HI) (Roth et al. 1996). These authors have found that IBI and HI are strongly correlated. IBI and HI were negatively correlated with the extent of agriculture but positively with wetlands and forests. Local riparian vegetation was a weak secondary predictor of stream integrity. This study emphasizes the importance of using multiple scales to assess environmental quality.

More recently, thanks to a more intensive use of GIS facilities powered by a better knowledge of landscape processes, landscape evaluation is assuming the role of a tool for holistic regional planning. For instance, Bastian (2000) has classified the German Federal State of Saxony by describing landscape units and has then evaluated the individual suitability for human activities, the functioning of the natural balance and the carrying capacity.

## 7.3 THE CULTURAL LANDSCAPE

### 7.3.1 Definition

There are many definitions of Cultural Landscape. Pertaining to this type we consider a landscape that has been changed in some part by a long-term human disturbance regime by which a unique assemblage of patterns, species and processes has been created. Thus, a cultural landscape is a human-dominated landscape in which the patch arrangement, their quality and function have been a mediated result of millennia of feedback between natural forces and humanity. Cultural landscape reflects the interactions between people and their natural environment and is a complex phenomenon with a tangible and an intangible identity (Plachter & Rossler 1995). In 1991, the UNESCO Secretariat proposed guidelines to identify a valuable and endangered cultural landscape: "an outstanding example of a cultural landscape resulting from associations of cultural and natural elements significant from the historical, aesthetic, ethnological or anthropological points of view and evidencing a harmonious balance between nature and human activity over a very long period of time, which is rare and vulnerable under the impact of irreversible change" (reported in von Droste et al. 1995).

Recently, the Council of Europe has proposed a European Landscape Convention (http://www.coe.int/t/e/Cultural_Cooperation/Environment/Landscape/) in order to promote the preservation of valuable cultural landscapes across the whole of Europe that is exposed to an unprecedented human disturbance regime. In the preamble, the Convention recognizes the role of the landscape as producer of "...local cultures and that it is a basic component of the European natural and cultural heritage, contributing to human well-being and consolidation of the European identity". This declaration can be extended to all the landscapes across the world in which people have for long time interacted in a "sustainable way" with local bio-ecological entities and aggregations.

Generally, these landscapes have a complicated structure represented by fine-grained mosaic in which physiotopes have been well localized and utilized in different way by agriculture, forestry and pastoralism. Often, slopes are transformed into terraccetes that strongly reduce soil erosion and facilitate agriculture practice by improving the retention of nutrients available for crops. Cultural landscapes can represent a good as model to test the possibility to expand humanity in natural environments without dramatic resource depletion and irreversible habitat perturbation (Antrop 1997). This could represent a utopian perspective but the lesson that cultural landscapes is teaching us should not be ignored. These perspectives are an urgent necessity and not an option to find a balance between human healthy development and sustaining the ecosphere (Halladay & Gilmour1995; Firmino 1999).

### 7.3.2 Interaction between natural and cultural landscapes

Any cultural landscape is the product of changes occurring in natural landscapes due to long-term human influence.

Human intervention in a landscape can be observed directly by the modifications that the landscape directly experiences. Often, human actions do not have a constant intensity and "efficiency" in landscape modification but still remain in a "non-genetic" memory, for instance, in the place's name and in the names of geographic emergences. For instance, Sousa & Garcia-Murillo (2001) have used the place names as an indicator of landscape changes in the Doñana natural Park (Spain) (Figure 7.2). Although ecologists can experience difficulties in the interpretation of place names, they have found a good correspondence between changes in land use and in the way the changes are perceived. A cultural landscape requires human stewardship to be maintained and, for this reason, it is fragile and comes back to a "natural" shape when human interference vanishes or is reduced. When land abandonment occurs in a cultural landscape, the transformation influences the structure of the landscape; terraccettes are generally progressively broken and fertile soil is lost by water erosion. Livestock are generally used after agriculture abandonment to maintain some openness in the landscape; this greatly contributes to terrace wall degradation due to trampling. In the Mediterranean area, deer and wild boar participate in this demolition. Relevant differences can be found on

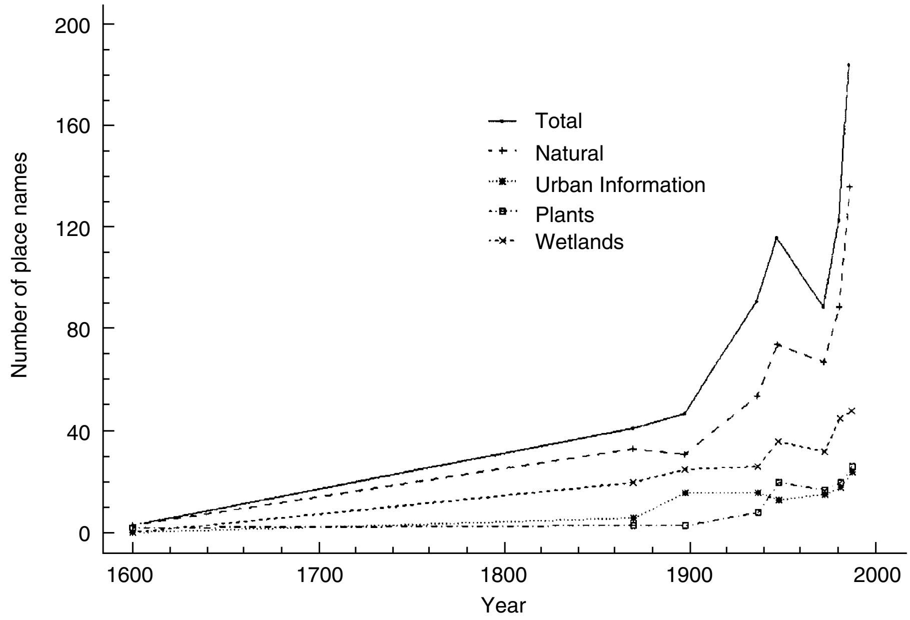

*Figure 7-2.* Changes in place names from 1700 onward in the Doñana Natural Park. The increase of place names is an indicator of a more intense use of this region in the previous century. Before that time the natural conditions of this land were less favorable for permanent human settlement (from Sousa & Garcia-Murillo 2001, with permission).

comparing natural and cultural landscapes. The structure of cultural landscapes is often more patchy than natural landscapes or more homogeneous. In cultural landscapes it is the intermediate level that is often lacking. However, in effect it is not possible to make any generalizations for these cases. Cultural landscapes have a more linear structure, such as hedgerows, or open spaces, than nature-shaped landscapes. But in some cases it is exactly the opposite. A desert oasis has more plants than a natural desert spring, and mountain farmland has less trees than a mountain forest but more trees than a natural mountain prairie. There is an infinite number of types of cultural landscapes around the world but all have in common patterns created by local traditional use of land and of their resources with a preservation strategy. This sustanaibility in such landscapes is a matter of time, however, and can persist for a limited time variable according to the different regional histories. Cultural landscapes are generally created by a feedback of trials and errors of sedentary populations but there are no reasons to exclude landscapes modified by nomadic populations as in the Mongolian steppes. In this last case, sustainability is assured by a shifting grazing mosaic of livestock and the stewardship is manifested not by digging the soil or pruning trees but by maintaining light livestock grazing, thus reducing, trampling and biomass consumption impacts. Some regions of the Earth, like the Mediterranean, can be considered a cultural landscape. In this region, the long-term interactions of populations and environment have produced irreversible changes in biological as well as ecological diversity. In many regions, land use changes and/or land abandonment have produced heavy modifications in the cultural landscape and the disruption and the vanishing of these valuable landscapes is a concern for authorities. The birth of countryside heritage centers is a timid reply to a diffuse problem of land management that in the present technologically-oriented landscape seems a difficult solution (Naveh 1995a; Antrop 2005). Often the cultural landscape supports, at least in Mediterranean Europe, more species than a natural landscape and in other cases the degradation of the cultural landscape is producing a low-quality landscape in which there is species decrease (Farina 1995). We have to be careful when we consider the “natural” value of the landscapes. In regions like the Mediterranean, the biodiversity was depleted thousands of years ago and there are no “new” species that can colonize empty “mosaic” niches.

Traditional management of landscapes, especially in the Mediterranean Basin, is indicated by Moreno & Vullafuerte (1995) as an important land practice to conserve large predators.

The value of reconnecting human culture with natural values in order to recreate a familiar valuable landscape has been discussed by Meurk & Swaffield (2000) for a rural area of New Zealand. These authors recognize the importance of reducing the gap between a mentality and a policy that maintains separate agri-business lands (composed of exotic species) from natural protected ranges. This allows the creation of a new landscape in which local identity (cultural and biological) can be integrated with the needs of marketing agriculture. This conceptual model looks very interesting and could find applications in many other countries afflicted by the same problem of oversimplification of landscape mosaics by agricultural intensification.

### 7.3.3 The fragility of the cultural landscapes

We have remarked that cultural landscapes are fragile and that they need human stewardship to be maintained. During the land abandonment process, especially in dry regions, the gradual evolution from an anthropogenic patterning to a more natural mosaic is disturbed by fire occurrence. Fires are a very common disturbance factor in the Mediterranean basin and in general in all dry regions around the world. Although most of the Mediterranean plants are fire tolerant and many require fire to complete their life cycles, in most of the Mediterranean basin the increasing frequency of human-induced fires is dramatically reducing the capacity of the system to incorporate the disturbances. In many cases, large areas are deforested and soil is exposed to erosion during heavy rain periods. Apparently, the presence of roads encourages such types of fires but also land abandonment. How to control these fires? In the Mediterranean, fires can be controlled by evaluating the economicity of woodlands. This seems a very simplicistic remedy but in many cases it is the reality. Along the northern Apennines, there is much evidence that the fire frequency has collapsed in the last decades when, due to the oil crisis, logging activity has again become profitable and woodlands have been discovered as an important source of income. Logging activity in this region consists in clearing young stands (25–50ys ) of variable size, generally between a few hectares to a maximum of 20–30 Ha. In this manner, at one time, a limited portion of soil is exposed and the successive year a luxuriant secondary growth recovers the understore, preventing water flashing. In this manner, dense homogeneous woodlands are transformed into a checker board of woodlots of different ages, structures and resource availabilities. The availability of cadastral maps allows us to predict the heterogeneity of woodland in many parts of the northern Apennines, creating a wonderful tool, especially if the historical information on the old cadastral maps is compared with the actual situation, using GIS facilities.

### 7.3.4 The cultural keystone species

Recently, Garibaldi & Turner (2004) have defined a new category of keystone species, the cultural keystone species, as species that play a special cultural role. Definite species are used to broadly characterize habits, food, handicraft, language, typology of settlements, tradition, etc. In some cases, cultural keystone species are the main drivers for cultural landscape structuring. For instance, the sweet chestnut (*Castanea sativa*) is a keystone species that requires the spatial arrangement of specific groves and infrastructure to dry and grind the fruits (Figure 7.3).

### 7.3.5 Landscape indicators

In order to evaluate processes and patterns that emerge from the analysis of landscapes, there is a broad array of physical and biological indicators. For instance, roe deer and earthworms have been used by Grossi et al. (1995) to analyze the effect of agriculture abandonment in the French Intermediary Alps.

The effect of landscape structure on biodiversity seems a very promising approach in evaluation and sustainable conservation management. Dauber et al. (2003) have investigated the landscape diversity and distribution of some focal land use in order to predict the diversity of groups like wild bees, plants and ants.

Hoffmann et al. (2003) have used the landscape mosaic as an indicator of bird species diversity in agricultural landscapes. In particular, the use of distribution of edges and small water bodies interdispersed with a farmland mosaic can be used to promote biological diversity at the individual farm level.

*Figure 7-3*. A sweet chestnut orchard, a common pattern along the northern Apennines cultural landscape (Tuscany, Italy).

### 7.3.6 Predictive landscape models

Landscape patterns can be used to build predictive models for threatened species. Lawler & Edwards (2002) have built an accurate predictive habitat model for six cavity-nesting birds (red-naped sapsuckers (*Sphyrapicus nuchalis*), northern flickers (*Coloptes auratus*), tree swallows (*Tachycineta bicolor*) and mountain chickadees (*Parus gambeli*) in the Uinta Mountains of Utah (USA) using 14 landscape metrics (see Table 7.1).

## 7.4 PRINCIPLES FOR LANDSCAPE MANAGEMENT

### 7.4.1 Introduction

One of the main goals of the landscape ecology is to study the structures of the spatial mosaic and their effects on ecological processes. Organisms, energy and resources are distributed patchily in the environment and this distribution has relevance for most ecological patterns and processes. Complex mosaics are crossed by organisms, energy, nutrients, water and disturbance processes and all these elements are influenced by landscape heterogeneity. Landscape ecology studies the complexity created by unequal distribution of energy, resources, organisms, predatory risk, populations and communities. Even a bottle of pure water is not homogenous; if we could track every molecule, each molecule has a specific energy and is influenced by neighboring molecules. As argued by Noss et al. (1996), the managing of species site by site or

*Table 7-1*. Landscape metrics utilized to assess the landscape suitability for four cavity-nesting species of birds in the Uinta Mountains of Utah, USA (from Lawler & Edwards 2002, with permission).

| *Label* | *Landscape Metric* |
|---|---|
| Aspen | Area of aspen (ha) |
| Willow | Area of willow (ha) |
| Open | Area of meadow and willow (ha) |
| Cut | Area of logged forest (ha) |
| Edge density | Meters of aspen meadow edge per hectare of aspen |
| Aspen interior | Area of >30 m from a meadow edge |
| Patch richness | Number of different types of patches |
| Contagion | A measure of how clumped the patches of vegetation are (0–100%) |
| Patches aspen | Number of patches of aspen |
| Patches willow | Number of patches of willow |
| Patches open | Number of patches of meadow and willow |
| Largest patch aspen | Largest patch of aspen (ha) |
| Largest patch willow | Largest patch of willow (ha) |
| Largest patch open | Largest patch of meadow and willow (ha) |

managing ecosystems species by species are no longer promising approaches. Landscape ecology considers sites not isolated each other and recognizes that scaled investigations are definitively a more intriguing and powerful approach to understanding their complexity (Haber 1990). In fact, homogeneity and heterogeneity are two different ways to see the environment. Homogeneity is often referred to the quality of adjacent patches as when we distinguish prairies from forest from a satellite image classification, but if we just look at the prairies level, using aerial photographs, this environment appears heterogeneous for some characters. Landscape scale represents one of the more efficient approaches to managing the ecosystems. In fact, the landscape–*sensu stricto*–embraces a large piece of land where most of the natural and socio-economical processes occur. And a landscape can be considered the main container of most of the patterns and processes that are of our interest. The landscape scale considers watershed or other units like ecotope, micro, meso, macro and megachore as the fundamental areas on which to determine to direct management actions. Often, the landscape hierarchy is easily overlapped by social and administrative bounds. For instance, in Italy and many other

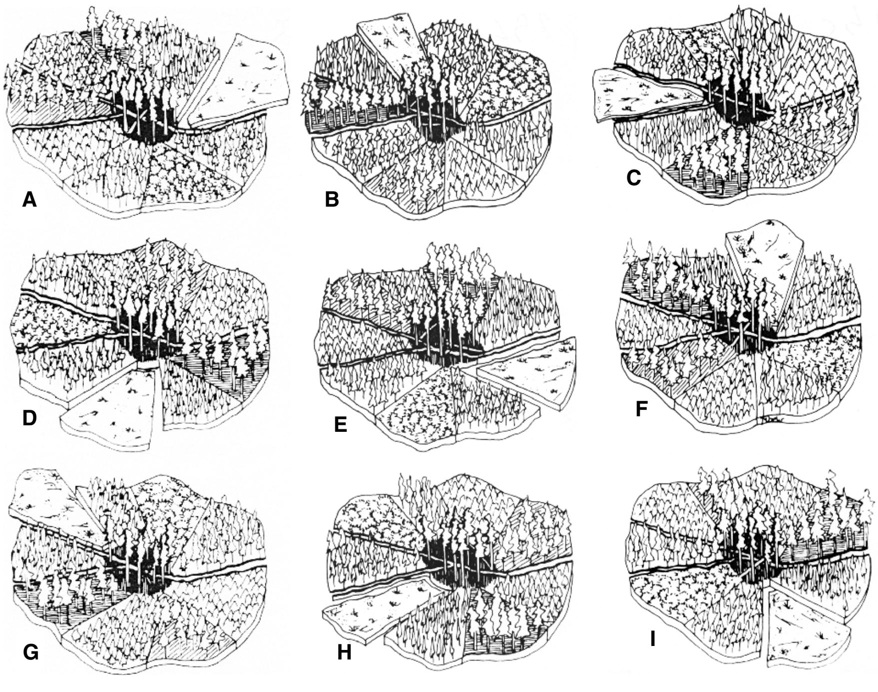

*Figure 7-4*. Long-term logging rotation to mitigate fragmentation of old-growth forests (Pacific region, US). This system should assure that almost 66% of the surrounding forested buffer is more than 100 years old. The 33% regeneration area will play the roles of foraging and habitat for successional species (from Harris 1984, with permission).

countries in Europe, there is a good correspondence between landscape hierarchy and social and administrative entities: ecotope/field/cultivation, microchore/farms, mesochore/parish/communes, macrochore/provinces/regions. In a few years, the land managers and conservationists have shifted from an autoecological approach to a synecological one and, finally, to a landscape management approach. In some literature, this last approach is called the ecosystem approach but clearly, when you read the contribution you can deduce that the authors were dealing with the landscape. The landscape approach assumes so great an importance in land management because human action in conservation, restoration and management is at a landscape scale.

Possible action at a large scale changes, according to the context in which the action is located. In agricultural landscapes, the heterogeneity (patchiness) of the mosaic requires specific actions to reduce the dramatic differences between the different land covers. Ecotones appear sharp and highly contrasted. It is in this context that landscape ecology was born and under this substrate that theories like island biogeography and metapopulations have been extensively applied. But when we change the scenario, moving into a forested landscape like the bottomland hardwood forest ecosystem (Wigley & Roberts 1997), the context is quite different. The mosaic is represented by the different age, structure, area and shape of the stands. Landscape patterns are highly dynamic and ephemeral. All the principles that we have labelled are less evident. Nevertheless, human intervention in such a landscape can create new conditions in forest succession and a scale some degrees higher than tree gaps and lower than tornados or wind storms can be intercepted by rare or habitat specialist species.

For instance, Miller & Urban (2000) have pointed out the consequences of fire supression on the connectivity of fuels with effects on fire patterns and behavior. Connectivity was found to be inversely related to fire frequency. Fire regimes are strongly affected by local conditions caused by human use of the land and, consequently, by the structure of the land mosaic.

In the Phoenix metropolitan area, Hostetler & Knowles-Yanez (2003), studying the relationship between birds and land, using categories at ten different scales of resolution, have found that bird distribution is strongly affected by the individual ownership tenure. Birds seem to react more to quantity and type of tree planted than landscape design and management.

### 7.4.2 The importance of watershed scale management

Watershed scale seems a very appropriate approach to efficient land management. A watershed may be considered as a multi-functional unit in the landscape and unique processes like water and mineral fluxes are distinct. The case of Fymbos in the Region of Cape Town perfectly fulfils the concept of catchment management. Recently, Fymbos vegetation, unique and spectacular flora, has been threatened by alien plants that produce an increase in biomass. This produces a decrease in runoff from the catchment area (van Wilgen et al. 1996). The invasion of European, North American and Australian weeds has created a complicated situation in which fire has no control of the invading plants. Fire regimes that occur regularly in this area find a greater fuel source, producing more severe consequences for plants. These fires produce a degradation of the landscape increasing soil erosion. This erosion is also increased by the lost of indigenous fire tolerant plants, that cannot protect the soil by a rapid recovery. One consequence of this landscape change is the reduction of water availability for the lowlands. In this case, managing the environment at the watershed scale should reduce the invasion of alien species, a reduction in fire severity and, a reduction of water consumption by plants and, consequently, more water availability for the environment and people in the lowlands.

### 7.4.3 The role of keystone species in landscape management

The term keystone species was used for the first time by Paine (1966, 1969), while studying the rocky intertidal zone. A keystone species plays a fundamental role in shaping and structuring a community. From this original definition the concept has been enlarged to include processes (Table 7.2). The role of keystone species in the landscape may be of great importance. For example, the buffalo herds of the Great Plains have modified the landscape, creating open spaces, trails and reduction of grassland biomass. The same occurs in African savannas where manure, urine, defoliation and the trampling of huge numbers of

*Table 7-2*. Categories of keystone entities and the probable effects of their removal (from Mills et al. 1993, with permission).

| *Keystone category* | *Effect of removal* |
|---|---|
| Predator | Increase in one or several predators/consumers/competitors, which subsequently extirpates several prey/competitor species |
| Prey | Other species more sensitive to predation may become extinct; predator populations may crash |
| Plant | Extirpation of dependent animals, potentially including pollinators and seed dispersers |
| Link | Failure of reproduction and recruitment in certain plants, with potential subsequent losses |
| Modifier | Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular successional habitats and resources |

large herbivores maintain the open structure of savanna. When a keystone species vanishes for natural or human-induced causes, many species collapse and landscapes change. In management policies, keystone species also have to be considered for their relatively inexpensive use.

Management procedures and models should take into consideration the cultural and economic changes that occur in society. This could have a great impact, for instance, on the plans to manage forests, as recently discussed by Bresee et al. (2004) for the forests of the Chequamegon National Forest, Wisconsin (USA), or the floodplain-river systems (Thomas 2003).

## 7.5 NATURE CONSERVATION AND LANDSCAPE ECOLOGY

### 7.5.1 Introduction

Nature conservation generally mobilizes energies focusing on a specific piece of land and distinguishing two main types of protected areas: the National or International Parks and Reserves.

National/International parks are heterogeneous areas in which generally different biotopes are present and in which some processes are conserved. Reserves are generally patchy and of a smaller size and surrounded by an agricultural or developed matrix.

Nature conservation plans are generally achieved by following three main approaches:

Conservation of threatened plant and animal populations.
Conservation of representative biotopes (a piece of land with a particular type of nature), including communities and ecological processes.
Conservation of areas with high biological and/or ecological diversity.

Generally, conservation policies tend to conserve structures more than processes. Landscape ecology can be useful for nature conservation because this recent discipline takes into consideration the spatial arrangement of habitats (Fairbanks & Benn, 2000) and, consequently, it considers structures and processes as they are perceived by the different species The perception of a landscape by the different species is often not coincident with the human perception and this creates difficulties when management actions are carried out (see also the cognitive landscape in Chapter 1). A compromise should be found, considering that in the future, wild, remote and large areas will be more and more rare due to human intrusion. While the use of indicator species appears difficult, the selection of guilds as management units seems more appropriate (Wilcove 1989).

The loss of natural areas is a diffuse trend around the planet and the preservation of valuable habitats or biotopes is achieved by preserving small remnants of such landscapes. Some reserves represent an archipelago of surviving habitats but are often islands in a matrix of agricultural or developed areas. With isolation can arise the risk of stochastic extinction. Species generally need different types of habitat along their life cycle and often, this is not provided enough in reserves, also because reserves are bounded by artificial, human-transformed landscapes. The high contrast between reserve patches and the surrounding matrix could create climatic stresses, especially at the edges, a concentration of predators and more influence of alloctone species on indigenous ones. Intensive agriculture in the matrix will offer new resources to reserves than extensive agriculture and forestry. A change in keystone species either the bottom keystone species (plants) or topkey stone species (predators), the first for climatic change and the second for landscape alteration, can modify the overall community. Several examples are proposed by Hansson & Angelstam (1991) on the consequences of fragmentation and isolation of forest areas in a cropland landscape. Predation increases the influence of seed consumers, like mice and can reduce the regeneration capacity of the forest. Some species that are keystone species, like woodpecker, that hollow of holes in trees and allow other hole-nesting species to breed in small forests plots, encourage the settlement of jackdaws (*Corvus monedula*) that is fully dependent on agricultural landscapes. Small remnants of flower-rich meadows have a low number of impollinators (hymenopterans and lepidopterans), and this produces a cascade effect on the plant community. The number of herbivore insects on blueberry (*Vaccinium myrtillus*) is higher in wet, interior forest patches. This is probably due to the palatability of this plant compared with lighter, drier forests (low content of carbon-based phenolics, which are antiherbivore substances). The abundance of insects favors the presence of insectivorous birds such as flycatchers and grouse. The destruction of wet forests affects many guilds and animal assemblages.

### 7.5.2 Landscape principles for natural reserves

Some basic principles for creating and maintaining natural reserves are unanimously agreed (Robinson et al. 1995):

Species richness increases with forest area. This is especially evident in tropical areas subjected to forest clearing for agricultural exploitation. In temperate biomes forest remnants also, have more capacity to conserve their biodiversity at reasonable levels.

A continuous area has more native interior species than two or more small ones. This principle is especially true in North American temperate and boreal forests.

In a forested area, patches close each other support more species than patches that are farther apart. This principle is in line with the concept of connectivity.

Disjunctive patches connected by strips of protected area are preferable to fully isolated patches.

Circular reserves are better then elongated ones because the portion of interior habitat is larger than in elongated ones.

These principles, in turn, recognize the importance of area, patch shape, connectedness and edge development attributes of the land mosaic studied and modeled by landscape ecology.

Finally, the rural context in which often protected areas are inserted plays a primarily role in the conservation of organisms like birds that require a broad range suitable matrices (Pino et al. 2000).

### 7.5.3 Disturbance regime and reserve design indications

The main concern in nature conservation is the perpetuation of species, populations, communities and processes. Recently, new approaches have focused on the perpetuation of landscape forms and processes.

Conservation planners have to consider all levels of biological organization, from population to landscape. Landscape structure appears to be becoming more and more important for nature conservation. In particular, large disturbance regimes seem fundamental for maintaining ecological processes (Baker 1992). Disturbance occurs in all biomes and its role in maintaining structure at species, ecoystem and landscape scales is more and more recognized. The effect of disturbance in the landscape mosaic has been discussed extensively in Chapter 3.

Disturbance regimes find a growing importance in reserve design and management. For instance, Moreira et al. (2001) suggest that to preserve bird diversity in Portugal, it is necessary to preserve agricultural lands and deciduous forest but prescribed fires and grazing are also indicated as parallel actions.

Baker (1992) focuses on some general principles where disturbance regime represent an important component for maintaining and perpetuating target patches and landscapes. To preserve species and processes it is necessary to have enough space in which natural disturbances can interact with ecosystems and the space is necessary to assure the shifting of regeneration patches and the movement of species from different quality patches. According to the source-sink model, it would be strategic to localize the source areas for a species and manage this source area with special attention. The preservation of climax communities can be assured by buffering them with successional stages. The biodiversity will be high although this represents a mimicking of natural conditions lost with human clearing and cultivation. It is clear that the best conservation strategy is to preserve large natural areas, but often this is a utopia and we are faced with remnant isolated patches. In this case, the conservation of small areas may be also important, but studies on the species-specific ecology habitat requirement are necessary. In this sense, landscape ecology, with the capacity to focus on the entire system composed of crops, developed and natural mosaic, is of great utility, taking into account more variables than the local perspective of nature conservation. One of the preliminary requisites to designing a reserve is that it contains a "minimum dynamic area", that is the smallest area in which under a natural disturbance regime, internal recolonization sources are maintained. This means that the area should have a family of disturbance patches with a temporally stable structure, and the incorporation of disturbance in the reserve bounds. In other words, the spatial arrangement of the disturbed patches changes but the overall structure of the landscape is maintained, creating a steady-state shifting-mosaic. If the goal of management consists in maintenance of the disturbance regime, it is important to have an area enough large to incorporate the greatest disturbance. For this reason, the choice of clusters of small reserves seems less favorable to maintaining internal disturbance dynamics. In order to design a reserve composed of core, buffer and transition areas (Harris 1984), it is important to avoid that these reserves become islands in an ocean of intensive human use. Some contradictions arise when such a model is compared with two different goals, the goal to maintain high diversity in the reserve and to assure the disturbance regime (Figure 7.5). The buffer for maintaining the disturbance regime should be, for instance, a secondary succession close to old growth forest in the reserve. However, in terms of species conservation, this buffer area could increase the number of alien species and habitat-tolerant predators. The same fire risk is higher if a buffers of shrublands is encircling a core area. But in reality, the role of buffers should be to mitigate the undesired disturbance and contemporarily to be an area in which to manage disturbances. In the geographical choice of reserves, it is important to place reserves where the disturbance initiates and also to include the areas in which disturbances naturally extinguishes. The first requirement is necessary for managing disturbances and the second to "politically" maintain this regime. In fact, if the fire regime in a reserve has continuity with urban suburbs or managed forests, it is clear that this regime will never be adopted. For example, to maintain flood disturbances, it is necessary to include in the reserve the upstream watershed where disturbances initiate, but also the downstream basin, where the disturbance (in this case, flood) is exported. In conclusion, in order to include or maintain disturbance regimes in a reserve, it is necessary to include the areas in which disturbances initiate and the areas in which disturbances naturally extinguish.

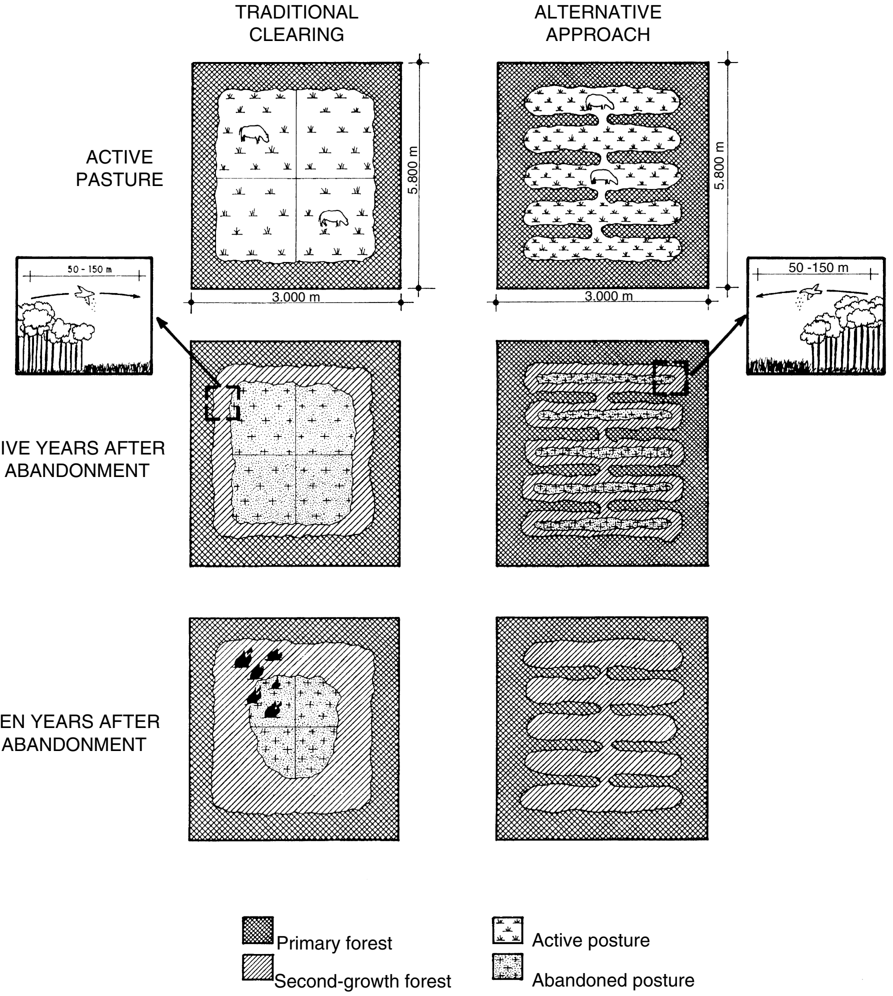

*Figure 7-5*. Schematic representation of "traditional" clearcutting in Amazonia compared with the recommended method to open small strips of forest connected to each other and large enough to assure grazing efficiency but early overflying by seed-disseminating birds (from Cardoso da Silva et al. 1996).

A boundary can be placed between a windward and a leeward slope for wind disturbance. For fire disturbance, a bare soil, a lake and streams seem good locations. Where there are no natural borders, human-made breaks can be provided for this purpose. Thus, the choice to locate forest reserves along riparian strips means that a fire regime is avoided. In this case, the strategy is the opposite and it appears clear that conservation is focusing on species along restricted temporal perspectives, transforming in this case the system into a habitat system. While strategies would be required to develop an ecosystem-level or landscape-level reserve system, these principles can also be exported to management outside the reserves, so as to maintain ecological diversity and healthy landscapes (Halladay & Gilmour 1995). For example, in the Mediterranean landscape logging, grazing and fires have shaped the cultural landscapes. In order to preserve these landscapes in places that are considered valuable, it is important to be sure that these regimes are still working. Recent land abandonment has changed these regimes and transformed a patchy landscape into one that is valuable and suitable for many species, in a more homogeneous system in which the disturbance regime has been modified. For instance, fire regimes are producing serious modifications in the system due to the high connectivity of these woodlands, connectivity that in the past was less due to the presence of several patches of fields. The green biomass was consumed by livestock and the fire risk was smaller that at present. Baker (1992) points out three main strategies to handle disturbances focused on nature conservation: surrogate, suppress, prescribe. To surrogate a disturbance means to use a disturbance that mimics another, for instance logging can mimic fires. But while size, shape, timing and spatial distribution can be surrogated, it is hard to surrogate the intensity and the final result can be far from expectations.

The suppression of a disturbance regime is a common practice in reserves. Fire, grazing and logging are generally suppressed. The suppression generally produces a coarse-grained landscape compared to a fine-grained landscape if disturbances are maintained. Again this is the example of the cultural landscape of the Mediterranean uplands (Farina 1996). The human disturbance suppression has created a coarse landscape, substituting the patchy, park-like mosaic *(coltura mista),* with homogeneous woodland stands. The suppression control changes the structure of the landscape. For example, a dam along a stream modifies the dynamics of the entire stream downwards, reducing disturbance by flooding.

The disturbance prescription is becoming a popular practice to manage natural prairies. But, due to the modest size of most of these prairies (especially in the US), fire prescription appears an insufficient long-term strategy, as argued by Baker (1992). Often the disturbance is produced in the same season and with a rotation to cover the entire area. Generally, this does not occur in nature. Thus, long-term effects are unpredictable. This regime can alter the distribution and behavior of species living in ephemeral patches created by a stochastic disturbance regime. And finally, small disturbances are not surrogates for a large disturbance. However, to maintain small reserves it is necessary to reduce the risk of large disturbances that could destroy the entire reserve. Intermediate transitional disturbance regimes could be utilized to manage systems in which fire suppression has created a biomass accumulation.

### 7.5.4 Inter-refuge corridor design

Often, corridors are utilized as frameworks to mitigate the effects of habitat fragmentation, although little data are available on the design effective corridors (Harrison 1992; Fleury & Brown 1997; Gilbert et al. 1998). Linehan et al. (1995) present a methodology to evaluate the ecological network of greenway planning. In mammals, natal dispersion is the more sensitive period in which corridor availability assumes an important anti-predator role. According to the predatory pressure, there are species that move very quickly from one group to another (deer) while other species, such as large carnivores, disperse until they find suitable unoccupied habitats. There are evidences that topographical features, such as mountain passes, rivers and lakes may locally affect dispersal paths but this information is not enough to predict the distance and direction of dispersion. If a corridor has enough suitable habitat for a species, it is reasonable to assume that individuals can disperse easily along the corridor. Other factors can play a role in the effectiveness of a corridor, for instance the seasonality of movement of males and females, the presence of human settlement, roads and other human artifacts, such as power lines, railways, aquaducts, pipelines, etc. Lindenmayer & Nix (1993) have studied the presence of arboreal marsupials in Australian corridors. These authors have found more individuals of larger species than small species in wildlife corridors. However, large marsupials are solitary and food opportunists. Small marsupials live in groups with colonial structures and consume widely dispersed food, so apparently narrow, linear-shaped corridors have no effect. A combination of habitat requirements has to be taken into account when corridor availability is considered. Lastly, the "context"of the wildlife corridor in the landscape is important. Corridors that connect gullies with ridges have more species that vegetation belts confined to a single topographical position, such as a midslope. Thus, the assessment of the site context, connectivity and the social structure, diet, and foraging pattern of target species appear to be important, at least for the animals studied by these authors. A single pattern or structure is not enough to explain the behavior of vagile organisms but it is necessary to take into consideration more structural and functional components at different temporal and spatial scale.

### 7.5.5 Hedgerows systems to conserve biodiversity in rural landscape

Hedgerows have been a very common pattern in many rural landscapes around the world but were actually strongly reduced by the "mechanization" of agriculture. Earlier, their role in maintaining diversity and stability of the systems was fully understood. Their structure is very different according to the functions and the regional cultural context considered, ranging from wind protection and soil conservation in Europe to medical or religious purposes in Asia. Their primary role is to divide properties, as enclosures for livestock, a domestic fuel source, and finally, serve as scenery complements. Generally, in traditional rural areas, they comprise a network that increases the connectedness between the different locations. Hedgerows play different roles in the landscape and are involved in many ecological processes acting at different scales. They can be considered, according to the perspective, as true habitats, ecotones, corridors and buffer zones for soil nutrients and managed fertilizers (Burel 1996). For instance, Clergeau & Burel (1997) have emphasized the role of linear rows of trees in a high degree of connection to the presence of short-toe tree creeper (*Certhia brachydactyla*) a small bird with a limited home range. At the landscape scale, hedgerows play a role in the control of water flux, nutrient leaching, wind flow and as barriers for animal and plant wind dispersion. Hedgerow planting programs are becoming popular, especially in Western Europe, after a dramatic simplification of the rural landscape of the previous decades (Jorg 1994). A recreational role is actually ascribed to many hedgerows systems and structures, which can mitigate deforestation in many countries. Finally, hedgerows can be as considered as structures from which forest regeneration can evolve quickly after land abandonment.

In countries like Denmark, a 2m-wide uncultivated border along streams is a statutory requirement, but this margin can be greatly improved by a buffer zone between fields and stream bank vegetation, although it is not easy to establish the magnitude of this buffer (Hald 2002).

Berg (2002) has discussed the effect of plantations of short-rotation coppices in open farmland. This author argues that such plantations represent a useful measure to stop the impoverishment of farmland biodiversity. Plantations increase the structural diversity of the landscape. However, in contrast, field plantation in forest-dominated landscapes produces negative effects. This result clearly indicates that the effects of every intervention change according the context in which we operate.

Landscape structure is an important element to be considered when biological control is adopted in agroecosystems. Thies & Tscharntke (1999) have experimentally demonstrated the importance of old field margins for the control of pollen beetle (*Meligethes aeneus*) on oilseed rape (*Brassica napus*). Parasitism was higher and crop damage lower than in landscapes with a simple mosaic. This has opened new perspectives for improving the biological control of managed landscapes.

## 7.6 CONSERVATION IN LANDSCAPES

### 7.6.1 Introduction

Most of the models used in landscape conservation have as a focal point the conservation of forests. This is particularly true for North American areas, in which the general assumption is that the presettlement conditions in eastern parts were characterized by dense forests. This model has also been exported into the European conservation arena (see Sutherland 2002 for a discussion). Open areas in temperate and boreal biomes have often been considered a human effect of deforestation. In reality, there are several evidences from the Neolithic age that large, open areas were present in Europe as well as in North America. The analysis of pollen and paleontological remains confirms this theory. In Europe, before agriculture (Holocene), open areas were maintained by a shifting mosaic of grassland and woodland created and maintained by herbivores such as moose, deer, wild boar, wild cattle and horses (Svenning 2002). Also, pollen remains confirm the presence of scattered open areas, often correlated with infertile soil and rock outcrops. The same situation can be observed in North America, and evidence also comes from distinct eastern races of open-area animals. This confirms the long-term persistence of open-areas in Eastern ranges. Two examples can be put into this discussion, the first is from the Netherlands, where in a recently created polder (an area of low-lying land which has been reclaimed from sea), domestic and feral grazers were introduced into woodland conditions. Unexpectedly, 60,000 grey-lag geese (*Anser anser*) arrived this site contributing to the maintenance of biomass removal. The mosaic created by this managed land also assured the presence of rare birds.

The second example comes from the Maremma Regional Park (Tuscany, Italy). This small park, created where the Ombrone river meets the Tyrrhenean sea, is a mosaic of coastal lagoons, pine plantations, Mediterranean maqui, unmanaged and managed pastures from reclaimed soils and crop fields. A feral population of Maremmana cows, horses, wild boar and roe deer are the most important grazers that maintain openness for wintering and migratory herbivorous and insectivorous birds.

Conserving biodiversity, water quality or other natural resources in a landscape is a hard task for land managers, due to the complexity and dynamism encountered at this scale. The social cost of maintaining landscape-oriented conservation plans is a central point in the recent debate. To preserve large animals and large ecosystems from extinction, considerable economic sacrifices are necessary, as reported by Mann & Plummer (1993). Conservation strategies can be activated using target species, populations and communities at the patch, landscape and regional scales. It is a common requirement for individual species to assure the adaptive size of habitat patches (grain size), homogeneity of patches (grain evenness), distribution of habitat patches (grain dispersion), matrix surrounding patches and connectivity among patches.

Under a more general umbrella of ecosystem health conservation, it is also necessary to consider phenomena that are usually pertinent to medical or epidemiological domains. It refers to the pandemic deseases that, like foot and mouth epidemics, one of the world's most economically important livestock diseases is an important factor for controlling the heterogeneity of landscapes, as recently discussed by Keeling et al. (2001).

"Defragmentation" is a process that occurs when a planting design increases the forest cover of a previously fragmented patch. In recent years, in the northern part of England and in the south of Scotland, extensive conifer plantations have reduced the fragmented status of forests. Hale et al. (2001) have investigated the effects of such management in British red squirrel populations. They found that this species uses "stepping stones" patches of habitat to move across the fragmented forests. With the increase of forest connectivity, the Scottish and Cumbrian populations experienced a "substantial genetic mixing", increasing the genetic flow speed.

The movement of populations in novel areas due to landscape modification by human use can create unexpected effects on such populations. It is the case of a population of dark-eyed juncos (*Junco hyemalis*) that breed naturally in mixed-coniferous temperate forests (1500–3000 in altitude). In the 1980s, a population became stable on the San Diego campus at the California University, under a Mediterranean climate. Sexual character signaling (the amount of white on the tail) declined by aproximately 22% compared to the mountain population. Pamela J. Yeh (2004) conducted an experimental verification, arguing that selection operating in a new habitat can produce a rapid evolution of selected sexual traits. This has strong implications in the general consideration that if humanity has often changed the landscape at every latitudine and spatial extension, "inventing" new landscapes, the actual biodiversity is in part the result of this long-term landscape manipulation.

The dispersal of diaspores is strategic to maintaining plant populations. Hence, Poschlod et al. (1996) argued that to achieve this equally it is not necessary to create static landscape infrastructures like corridors but "dynamic moving, ecological infrastructures", including domestic livestock. Many seeds are passively transported by aninals, especially birds and mammals and in order to maintain plant dynamism it is necessary to assure specific vectors for this and not only think that the wind is *per se* enough in the dispersion processes.

It should be considered that the grain size of patches is species-specific. Different species have different sensitivities to the above-mentioned characters. Species of deer, living in flocks, have a different perception of the habitat complexity when compared to solitary species. The habitat requirement can change according to the season, the physiological status, the age and the quality of the occupied habitat. Often the conservation of a target species can produce benefits to other species, especially if this species occupies a large portion of the landscape. The conservation of target species requires a very deep knowledge of the autoecology and often this is not available on the entire geographical range of a species. This remark is not just to discourage the target-species approach but to alert researchers to the difficulties that can be found by moving in this direction and that often more research is required in advance. Managing target species often means working in human-modified landscapes and further limitation and practical constraints, such as the property, the different regulations in the same region, or the overlap of management competencies. These difficulties are also common to other conservation approaches. The conservation programs in agricultural landscapes are increasing after the heavy impact of the high technology of the last decades. The aims in these landscapes are to maintain the biodiversity and to assure connectivity to fragmented sub-populations. The restoration of field margins is extremely popular at the moment and positive results can easily be achieved, especially with arthropods diversity. This has economic implications because often if a balanced invertebrate community is conserved there may exist more biological controllers for pest diseases. The conservation of vertebrates in rural landscapes can be achieved by increasing the margins and by preserving the woodland remnants, assuring good connectivity. The plantation of mixed woodlots seems a very promising strategy, assuring a broad spectrum of resources around the year and a more differentiated fauna. It is not possible to recreate natural patterns in farmlands but the conservation of remnants and the increase of connectivity, may be surrogates for a more natural matrix and may be good actions. Conservation in disturbed landscapes in which the mosaic heterogeneity has been depressed by human activity, may require a new disturbance regime. This approach seems very interesting although not particularly workable. Prescribed fire is one of the most used tools to assure heterogeneity in remnant prairies in the USA and to control biomass in coastal pine ranges. Although fires are relatively inexpensive tools, this practice can be difficult to handle when the managed areas are of limited size and the creation of an artificial checker board is not the optimal plan. It is not clear enough at the moment whether the habitat loss may be compensated by careful planning of the landscape. Explicit spatial models can be very important to achieve this goal but not all the species have a population pattern that can be manipulated spatially. The spatially explicit population models (see also chapter 6) are useful for considering both species-habitat relationship and the spatial and temporal arrangement of habitat patches. Generally, these models are arranged for one or a few species, the adaptation of these models to modeling biodiversity at the landscape scale represents a true challenge for landscape management (Turner et al. 1995).

### 7.6.2 Conservation of fragmented habitats and populations

The status of fragmented habitats and populations is very common in human-dominated landscapes and the survival of many species depends on the rate of connectivity between each fragmented habitat patch. Habitat patches have to be considered as heterogeneous in terms of area and quality. The relationship between patches in a landscape, the spatial arrangement, the temporal change in landscape structure and the dispersal characteristics of the species are important components of this scenario. Local populations can occupy a patch of the landscape and many local populations compose the natural population at a regional scale. Habitat patches may be considered as discrete areas used by a species uses for breeding or for obtaining other resources. Fluctuations in local abundance can produce local extinction but at the regional scale, if these local fluctuations are not synchronous, the risk of regional extinction is negligible. If extinction occurs in habitat patches, recolonization is an expected event after extinction. When we study this process at the landscape scale, it appears important to measure the landscape spatial structure defined by Fahrig & Merriam (1994) as the spatial relationship among landscape components. The characteristics of landscape spatial structures are:

Size, shape and quality of patches: larger patches have a higher persistence of a population. The dimension of a patch can influence the edge effect and the predator ratio. The size of a patch *per se* is not enough to characterize the degree of persistence of local populations because two patches of the same size but with different edge amounts and shapes can support a population differently. Patch quality also plays an important role. For example, the presence of old trees in a patch can increase the persistence of nesting-hole birds.

The presence of corridors through landscape. The function of these corridors consists in maintaining the connectivity between different local populations and there is much evidence of the importance of connecting structures such as fences, shrub strips, and road plantations to encourage the movement of animals.

The spatial configuration of the components of the landscape seems extremely important. In fact, the position of habitat patches in a hostile matrix seems more important than the dispersal routes. It also appears important to understand the rate of change of a landscape. If a landscape changes more rapidly than the rate of change of a population, the regional population will have difficulties in surviving. It must be clear that the value of small fragments of remnant habitats has to be scaled with the importance of all of an area and is not an alibi for reducing large patches of undisturbed lands. Nonetheless, it is important to recognize the role of small habitat fragments in preserving some species and its role is like that of a bank, to preserve genotypes more than landscape dynamism. Small areas have no possibility to support large mammals but can play a relevant role for plants and invertebrates (Shafer 1995). Small reserves have few chances to preserve a species for a long time and the biological diversity is lower than in the surrounding, undisturbed areas. Small reserves have been created to protect rare butterflies function for many decades, without apparent loss of animals. A fragment can be used as a core area for a restoration project! If a fragment is inadequate to preserve one species it could be enough for another and it is clear that small fragments may have a relevant role in a landscape. Managing small areas means that one can replicate these fragments in a landscape, protect them with buffer zones and connect them to each other by usable corridors. Although forest or prairie fragments are not optimal to develop an efficient long-term conservation policy; their presence may mitigate deforestation effects for many species of organisms, also in tropical regions (Turner & Corlett 1996). In these regions, fragmentation is more deleterious than in temperate and boreal forests due to the presence of more species intolerant to habitat changes. Several disturbances occur in fragments of tropical forests. Some effects are common to other forests, like the human disturbance of harvesting, the diversion of water courses for transporting the timber. Other effects are particularly evident in these fragments, like the edge effect, the change of microclima, drier and hotter at the borders. The loss of keystone species like large carnivores increases some species of small carnivores that, in turn, create a strong pressure on many prey species. Few rainforest species are tolerant to open spaces, and fragmentation increases the numbers of alien species that compete with the indigenous species. Despite these negative effects "fragments are better than nothing" (Turner & Corlett 1996; Fisher & Lindenmayr 2002). The presence of tropical fragments in agricultural landscapes greatly enhances the biological diversity (Nepstad et al. 1996). A realistic policy in rural Amazonia should assure forest remnants; this would be a very important step (Schelhas & Greenberg 1996). To increase this capacity, it would be important to assure a higher connectedness between patches. Fragments, in many cases, are enough to preserve invertebrate fauna and to assure the spreading of several plants. We can expect a species decline over time in small fragments, but these fragments could serve to provide opportunities to preserve some species from future extinction. The presence of fragments could recreate in the future, by coalescence, a new tropical forest cover, a process more difficult when starting from a bare soil. Cardoso da Silva et al. (1996) suggest mitigation actions during tropical forest clearing by reducing the size of clearcut pastures in order to increase the colonization capacity of forest trees after the 6-8 yrs of abandonment. They observed that especially frugivorous birds crossing the pastures can spread tree seeds, favoring forest recovery. *Ad hoc* legislation on the size and shape of deforested strips could strongly mitigate the effects of forest fragmentation (Figure 7.6). Most of the actual fragmentation in the tropics is driven by small-scale and time and economical constraints, and solutions to reverse this

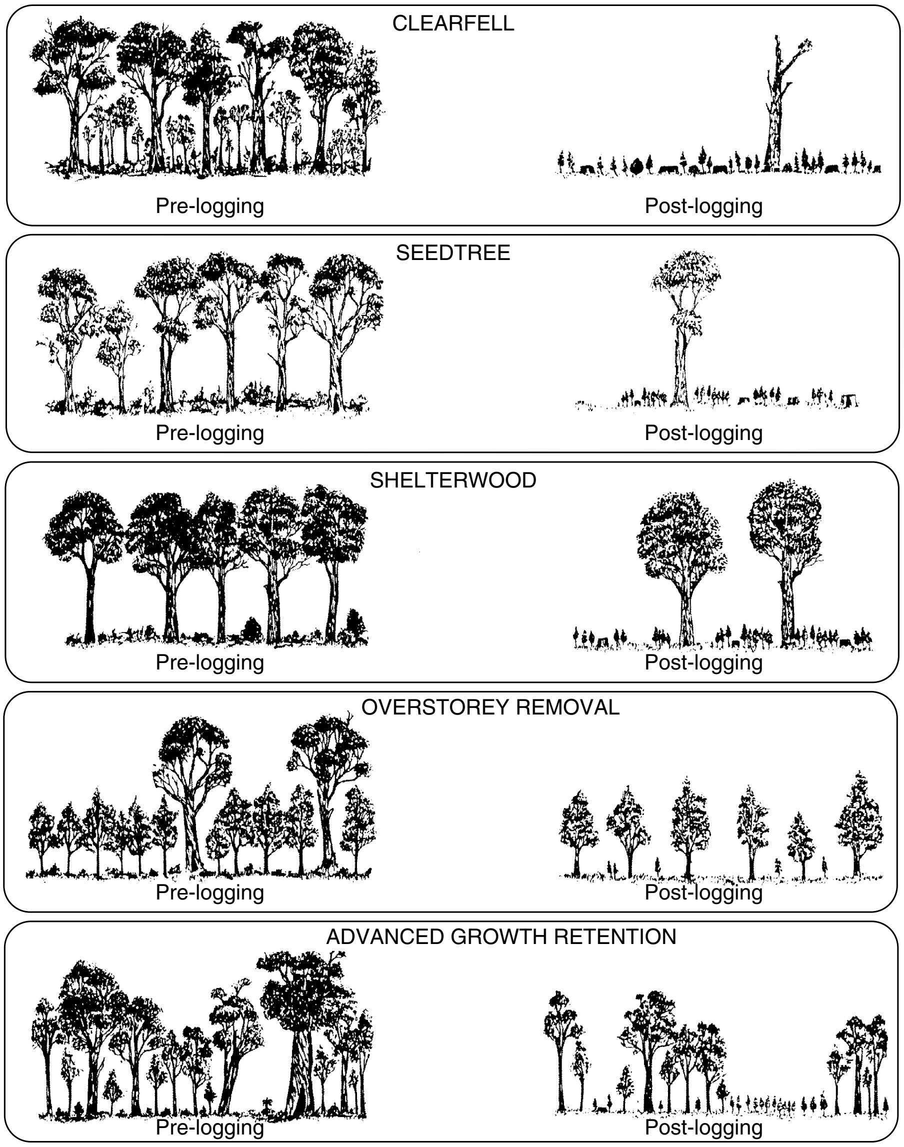

*Figure 7-6*. Silvicultural treatments : Clearfell, removal of all trees. Seedtree retention, 7 to 15 well-spaced trees per hectare; Shelterwood, logging is reduced to assure a good soil cover. Overstorey removal, logging of old trees in a two aged stands, reducing competition between two strata; Advanced growth retention, in a multi-age structured forest. All trees with good growth potential are retained (from Taylor & Haseler 1995, with permission).

*Table 7-3*. Herd size in the north of Brazil (from Hect 1993). It is possible to verify that cows have undergone a dramatic increase in most of the regions. These values may be used to evaluate the level of fragmentation of tropical forests in this country (from Hecht 1993, with permission).

| | 1970 | 1975 | 1980 | 1985 | % increase1970–1985 |
|---|---|---|---|---|---|
| Acre | 72,166 | 120,143 | 292,191 | 333,457 | 362 |
| Amazonas | 283,362 | 415,457 | 455,584 | 420,940 | 48 |
| Para | 594,313 | 777,660 | 2,729,796 | 3,485,368 | 486 |
| Rondonia | 23,126 | 55,392 | 248,558 | 768,411 | 3227 |
| Roraima | 238,761 | 246,126 | 313,069 | 303,501 | 27 |
| Amapa | 64,990 | 62,660 | 46,069 | 46,901 | –38 |

trend are not on the agenda. In Table 7.3 the herd size in the north region of Brazil is reported. The huge increase in deforested areas is evident. The pastures in tropical lands are not self-maintained as in temperate bioma. In the tropics, most of the nutrients cycle is maintained in the vegetation biomass. The soil has little capacity to retain nutrients, so after few years, the pastures are impoverished and grasses are substituted by unpalatable shrubs. Removing shrubs and adding fertilizer is possible but not convenient and new pastures are created by deforestation, in a type of "shifting ranching" (Hecht 1993). Most pasturelands older than 10 years are abandoned and transformed into degraded lands. In Australia, the maintenance of non-logged creeks and gullies seems a good strategy to conserve nocturnal birds and mammals (Kavanagh & Bamkin 1995). Silvicultural treatments, in eucalyptus forests in Tasmania has been discussed in terms of bird species' conservation. Logging retention seems a promising technique to reduce the impact of logging on the animal community. Tree retention produces lower density but the maintenance of high diversity is comparable to unlogged stands in bird assemblages (Taylor & Haseler 1995) (Figure 7.7). Temperate regions support fragmentation better than tropical areas, having species more adapted to the fragmentation constraint. Villard et al. (1995) have found in the fragmented rural area of Ontario that four target species of neotropical migratory birds have a population turnover due to the combination of many factors and that site fidelity is an important element. This research contributes to a long debate on the role of island size and isolation. The behavioral components of species can change most of our actual knowledge. Isolated woodlots are important when animals such as migratory birds are moving at the landscape scale. In east-central Illinois, Blacke & Hoppes (1986) found that small woodlots are important for migratory birds, especially if these elements are surrounded by large forested areas. The presence of many species during migrations confirms the ability of birds to colonize fragmented habitats but probably other negative factors, such as high predatory pressure, no tolerance to edges, more unpredictable microclimate, higher intra and interspecific competition are contributing to local rarefaction.

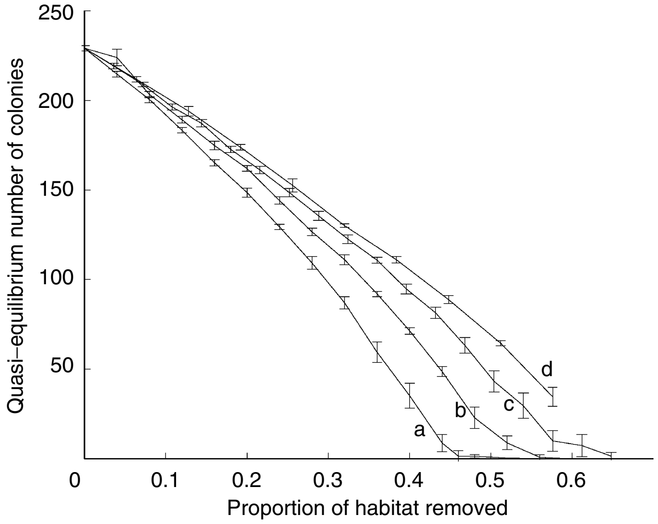

*Figure 7-7.* Proportion of the removed habitat and number of colonies of army ants at quasi-equilibrium. The habitat removal used different ways: a: 1 x 1 block; b: 2 x 2 non overlapping blocks; c: 3 x 3 non-overlapping blocks; d: 4 x 4 non-overlapping blocks (from Boswell et al. 1998, with permission).

Today, new tools are available to improve conservation policies like individually-based spatially explicit models that can predict the consequences of future land-use changes on populations of plants and animals. For instance Rustigian et al. (2003) used such a tool to investigate the effect of alternative landscape design of amphibian populations dynamics driven by climatic clanges and human demographic stocasticity.

The effects of habitat fragmentation are species specific and can be predicted by applying the percolation theory. This theory describes a change in the behavior of a percolating patch by means of a theoretical lattice where 0.5928 of the cells have been randomly removed (Stauffer 1985). Boswell et al. (1998) have predicted by using such a model the fragmentation threshold at which the army ant (*Eciton burchelli*) is extinct in a fragmented area (Figure 7.8). Simulating the fragmentation, they randomly removed cells from the theorethical lattice and with surprise they noted that ants go extinct already at the level of 45% of forested cells. This result has been interpreted as an unespected sensitivity of army ants to fragmentation. In fact, removing the same percentage of forest in a unique block, they observed that the population of ants remained stable. These results must be discussed in terms of conservation strategies. Often, we believe that corridors can be the solution in fragmented environments, but many species have no long-term memory for using known patches across fragments, neither

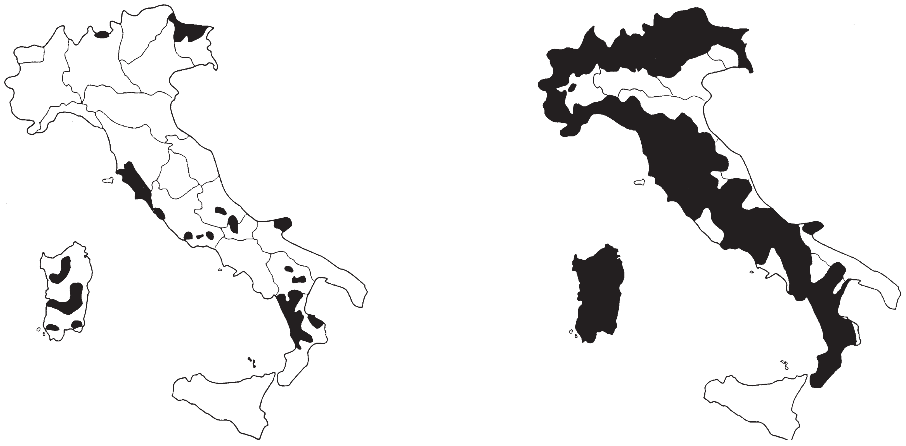

*Figure 7-8*. Distribution of ungulates *Cervus elaphus, Dama dama, Capreolus capreolus, Ovis musimon, Sus scrofa* at the beginning of this century (A) and the actual distribution (from Ghigi (1911) A, and Pavan (1983) B, quoted by Apollonio 1996, with permission).

do they have a global vision of the landscape in which they live. The authors suggest that it is better to remove large blocks of forest instead of narrow strips and this could increase the efficiency of a suitable forest management policy.

### 7.6.3 Conserving large carnivores

The conservation of large carnivores poses more problems in any conservation plan because the minimum area required by these mammals generally exceeds the availability of the reserve size (Noss et al. 1996). The traditional method of selecting discrete nature reserves is generally not enough efficient to protect the carnivore populations and these authors suggest a zoning approach, in which core reserves are surrounded by buffers and connected with other reserves by regional corridors (Figure 7.9). This model has three main elements: core area, buffer zone, corridors. The core area that represents a large wilderness, the low road density area that should play the fundamental role of a source. The second element is represented by buffer zones or zones of transition that can be extremely important for large home-range species. In this area, human activity is reduced and a political and social compromise assures only modest pressure on large carnivores. Finally, the corridors that should assure the movement of animals to guarantee genetic exchange between the metapopulations living in surrounding reserves. This model has a general potentiality and can be used in all human-dominated landscapes at different spatial scales. It appears important to also take into account the scale at which we are considering the connectivity. In

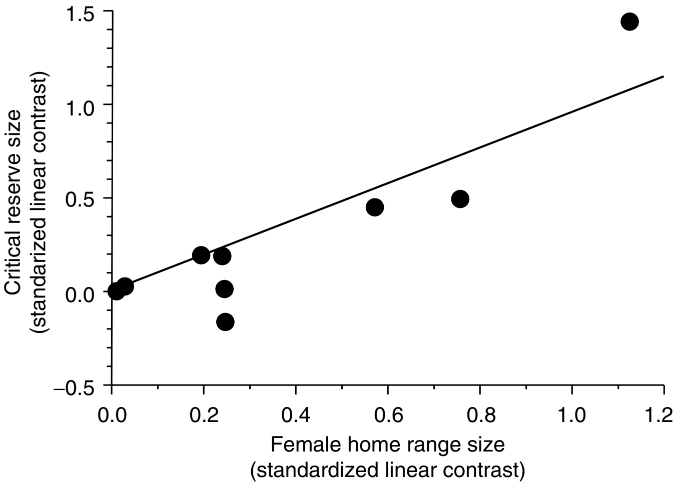

*Figure 7-9*. Relationship between critical reserve size and female home range size of ten large carnivorous ($r^2 = 0.84$, $F_{1,8} = 42.1$, $P<0.005$) (from Woodroffe & Ginsberg 1998, with permission).

fact conservation planners should consider the movement of individuals within the home range, dispersal between home ranges or between populations. The model source-sink, in terms of the quality of the considered habitat, seems extremely important for planning efficient reserves. Corridors again have not be considered as fixed structures of a landscape but as a functioning part of the landscape that change according the season, the species and the landscape disturbances. In some cases, the corridors preferred by large carnivores are the same parts of the landscape used by humans. Natural reserves considered as discrete and isolated entities in a human-dominated landscape cannot be a successful model to protect animals such as large carnivores. The need to manage the regional landscape seems a more promising approach in human-dominated systems. In Italy, the recent spread of wolves (*Canis lupus*) is a clear example that if connectivity is assured—in this case the land abandonment along the Apennines—it has created a huge system of secondary succession core areas that assure refuges and movement to this species. Contemporarily to the decrease of livestock (main food resource for wolves in the past) due to land abandonment, deer and wild boar have recolonized most of the mountain ranges from Alps to the Southern Apennines and islands (Sardinia, Sicily) (Figure 7.10). Extension of protected areas and density of large carnivores have not been found to be significantly correlated by Woodroffe & Ginsberg (1998). Population size is a poor indicator of extinction in large carnivores. Most of the mortality in carnivores is caused by human conflict at the border areas, which become sinks. The species under risk of extinction are the ones that persist in small reserves but that range widely (f.i., the Marsicano bear (*Ursus arctos marsicanus*), a highly endangered species that is protected only in a limited part of its home range) (Figure 7.11).

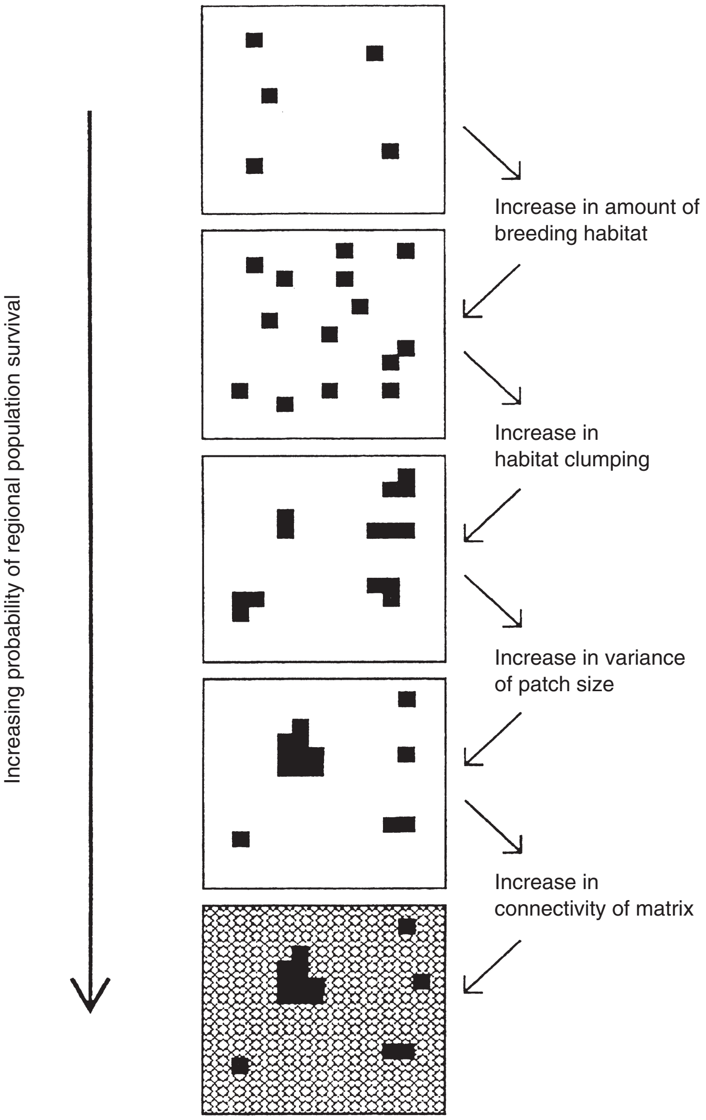

*Figure 7-10*. Predictive modeling of the effects of the landscape spatial pattern on regional population survival (from Harrison & Fahrig 1995, with permission).

### 7.6.4 Toward the conservation of processes: Western Paleartic bird migration

Conservation plans should take in account the maintenance of ecological fluxes more than focusing on the conservation of species. Often the presence of a species is ephemeral, linked to a particular stage of the ecological succession.

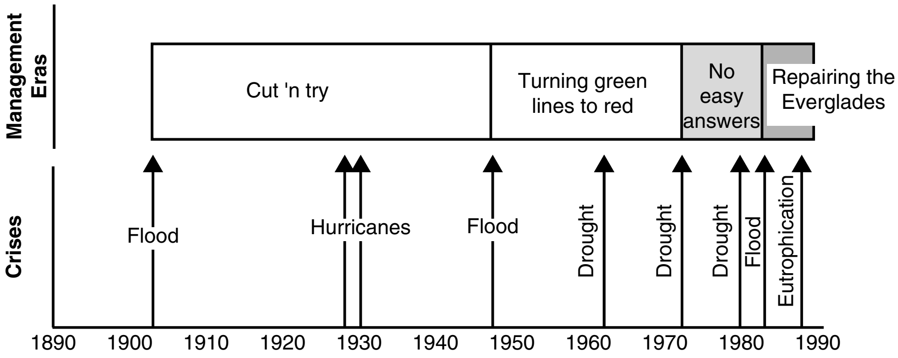

*Figure 7-11*. Historical processes shared between environmental crisis and management policy in the Everglades from 1980 to the present (from Gunderson et al. 1995, with permission).

In Europe, an important conservation goal should be devoted to migratory birds and to preservation of the environment along their routes. In each season, millions of birds move across Europe to the Mediterranean and the African continent, using different movement strategies from no-stop flying to stopover flight. Especially birds belonging the second group, require specific habitats to roost, refresh and forage in order to recover energy lost during the migration. Generally, for such birds open, park-like areas in which short grass patches are blended into shrublands and woodland and in which fields, pastures and woodland logging represent suitable temporary habitats. Many species are habitat specialists during the breeding period but during the migratory season, they behave like habitat opportunists. Large-scale migratory refuges are necessary to maintain these fluxes and this strategy requires strong political consensus among different countries. In this case, farmland and pastureland should be considered as priority valuable landscapes so as to preserve the migratory birds of the west-paleartic region. On the other hand, conservation of less vagile species requires strategies that should take into account the rehabilitation and creation of new source habitat patches for target species. Both these strategies are not in conflict with each other but compete for the required funds.

### 7.6.5 Landscape patterns and conservation

Landscape patterns are represented by the distribution in space and time of habitat patches and resources. Fahrig & Merriam (1994) have divided the landscape patterns into two broad categories: spatial patterns, and spatio-temporal patterns. In the first case, time is not considered important, at least at the time scale of the species investigated. In the second case, the landscape pattern changes over time and in space, for example a habitat can be ephemeral. Harrison & Fahrig (1995) consider six main components of the landscape spatial pattern:

Amount of habitat in the landscape
Mean size of habitat patches
Mean inter-patch distance
Variance in patch sizes
Variance in inter-patch distances
Landscape connectivity

In Figure 7.9, the increasing probability of population survival at the regional scale has been illustrated. If the temporal dimension is introduced into the landscape spatial patterns, we can expect changes of those patterns over time and ultimately the survival of a species is affected. Disturbance and permanence of a temporary or ephemeral patch are important factors. Disturbance can change the survival according to rate, size and temporal correlation in disturbance. Rate of patch formation and patch lifespan are important aspects of ephemeral patches. There is a general consensus that habitat loss (fragmentation) reduces the probability of survival of a regional population, but if patch size increases as does the inter-patch variance in patch size, this has a beneficial effect on the populations survival. In an ephemeral habitat, the survival probability increases if the patch lifespan increases, and in such a landscape, the spatial arrangement of the patches is less important, due to high dynamics.

## 7.7 LANDSCAPE DESIGN (CREATION) AND RESTORATION

A main goal of landscape ecology and restoration ecology is to identify key habitats and species, to assess distributional gaps and to process the best strategies for plants and wildlife, whilst at the same time guaranteeing recreational benefits to the society. Unfortunately, restoration projects for large areas are rare and this is an intrinsic limit in the application of landscape ecology principles.

However, in some cases, like in the restoring and design of ponds, their presence in clusters could provide more opportunities for meta-populations than a few large, isolated areas. Landscape design is an important component of practical landscape ecology, often recommended after an investigation on the environmental preferences of endangered species (Russo et al. 2002), but also for managing common species like rabbits (*Oryctolagus cuniculus*), which have a deep impact on vegetation (Calvete et al. 2004).

Generally, landscape design is considered an activity to rehabilitate degraded landscapes or modify landscapes after a change in land use, such as fields on urban fringes. The principles that guide landscape design are a synthesis between the human-perceived landscape and the ecological processes (Makhzoumi 2000). Modern landscape design grants visual patterns as the first choice in creating an harmonious view of the neighbors. This largely depends on the country-oriented sensibility that create recognizable British, Central European, Mediterranean-like landscapes. Landscape design in most of cases consists in planting trees and shrubs in appropriate quantities, shape and diversity, mimicking natural patterns and increasing the visual and structural complexity.

An interesting example is from the Negev landscape (Israel) in which six different native tree species were investigated in order to reduce the heat of solar radiation and increase biodiversity under shaded conditions (Kotzen 2003). Native species that do not require irrigation seems to be the best candidates to modify the human-induced desertic areas in an ecologically correct way. These actions in general are favorable to many species of plants and animals and produce new ecological processes. It is not often one designs a new landscape, but it is very popular to restore small areas utilized in the past as gravel mines or for industrial waste disposal. The variety of local conditions are too detailed but some general guidelines can be synthetically listed:

Select indigenous species of trees and shrubs.
Plant according to natural shapes and not in linear rows and never perpendicular to the contours.
Increase the edge-shape complexity, modulated by minor soil undulation.
Retain trees where possible. Scattered trees are important for wild-fauna.

Plant design should pay attention to the different habitat needs of target species in terms of soil, sunlight, sheltered or exposed sites. Landscape creation is a relatively recent practice although the “cultural landscapes” are beautiful examples from the past. However, a fundamental difference appears when we compare the past and the present landscapes. In the past, the landscape “reaction” was dominated by a balance between human input and land productivity by continuous stewardship. Today, most landscape management activity is focusing on wildlife conservation and scenic improvement. Many tools are available for ecological restoration and it is a common strategy to reinstate traditional management where available, but these actions are in many cases too expensive to be expanded to the entire landscape. Grazing, mowing and fires are common practices at local as at landscape scales. Grazing is particularly efficient and a relatively cheap method that can be used from lowlands to uplands. Fire is very efficient but not usable in all conditions and seasons, and more difficult to control when dry biomass has accumulated.

Deciduous forests in the eastern United States have been reduced in a few generations to their very lowest level. For instance, in order to guarantee the survival of these stands for future generations, Keddy & Drummond (1996) proposed an approach based on four steps:

a) Managing the remaining forest areas sustainably.

b) Restoring altered forests to their original composition.

c) Replanting deforested areas.

d) Protecting remnant primaeval areas as ecological models for research and comparison. To achieve these goals some descriptors were presented at the scale of stand and landscape (Table 7.4).

## 7.8 HIERARCHICAL STRUCTURE OF THE SYSTEM AND BIODIVERSITY CONSERVATION

Actually, conservation strategies are moving from static species or habitat-oriented policies to a more dynamic and "realistic" approach. In this direction, a fundamental contribution is made by hierarchical theory. The hierarchical approach to understanding natural systems (as described in Chapter 2) allows one to take into consideration, for conservation goals, the different composing subsystems, assuming different dynamics moving from the smallest (faster dynamic) to the larger (low dynamic) (Lewis et al. 1996). The goal of this approach consists in protecting the total diversity at the landscape level of ecological organization (Norton & Ulanowicz 1992) and to distinguish different policies according to the hierarchical scale selected. Before we explicitly explain these concepts, it is important to focus on the autopoietic capacity of the natural systems to be "creative". At every level, systems have the capacity of being self-sustaining throughout homeostatic and homeorhetic responses to changing conditions. This capacity assures the system will adapt itself to the new conditions. This capacity may be considered as a healthy status of an ecological system. Landscape scale seems essential in any biodiversity protection planning, surpassing the "false" myth of species conservation that must be considered a good start at small and medium scales. The biological and ecological (*sensu* Naveh 1994) diversity should be considered "dynamically in terms of healthy processes, rather then merely as the maintenance of current elements of the system" (Norton & Ulanowicz 1992). In this perspective, economy and diversity should find a meeting point. In fact, in a world dominated by humans, we have to discover mechanisms that enhance diversity, encouraging policies that in the last analysis, mimic the natural disturbance regimes (Figure 7.10). We can imagine socio-economic evolution (creative like the evolution of ecological systems) moving in parallel with the ecological one and presenting a trajectory shaped by reciprocal feedback. The socio-economic crisis of

*Table 7-4*. Main ecological descriptors used in deciduous forest in the eastern United States by Keddy & Drummond (1996) at stand (local) and landscape scale (from Keddy & Drummond 1996, with permission)

| | | |
|---|---|---|
| Stand scale | 1. Tree size defined in terms of basal area (mean diameter at breast height (dbh). | Three categories : normal (>29 $m^2$/ha), intermediate (20-29) and low (<20 $m^2$/ha). |
| | 2. Canopy composition. | In a mature deciduous forest the canopy is dominated by few species, while young forests have a higher tree diversity. In a mature undisturbated forest, shade tolerant species are dominant and intolerant occupies 2-10% of total forest composition. Increasing the disturbance shade-intolerant species are increasing. So, the percentage of tolerant species can represent a property. They distinguish three categories: control/normal (>70% of tolerant species), intermediate (30-70%) and heavily altered (<30%). |
| | 3. Coarse woody debris. | This material includes fallen logs, snags and large branches and is important for many species of organisms. The coarse woody debris in a forest depends on the history of the forest and generally increase with age. Three categories are proposed: control/normal (both firm and crumbling large log present), intermediate (either firm or crumbling large logs present, and low (large logs absent). |
| | 4. Herbaceous layer | Herbs are present in mature forests in gaps and clearing. This layer is particularly sensible to grazing. Three categories are suggested: control/normal (≥ 6 species), intermediate (2-5 species) and low (<2 species). |
| | 5. Curticulous bryophytes (mosses, liverworth and lichens). | Their presence in many cases enrich of Nitrogen the soil. Three categories are proposed : control/normal (≥7 species), intermediate (2-6 species), low (<2 species). |
| | 6. Wildlife trees. | The presence of large logs and trees with cavity enhance the forest suitability for animals (especially mammals and birds). Three categories are proposed: control/normal (≥ wildlife trees/10 ha), intermediate (1-3 wildlife trees /10ha), low (<1 wildlife tree/10 ha). |
| | 7. Fungi: macrofungi. | No quantitative data available. Probably a good indicator to develop in future carriage return. |
| Landscape scale | 8. Avian community. | Many birds are not sensitive to forest age, and often there are more species in intermediate aged stands than in old growth forest. But some species require a large forested area. These area sensitive species may be good indicator of stand size. Three categories are proposed: control/normal (≥ 5 area sensitive species), intermediate (2-4 species), and low <2 species). |
| | 9. Large carnivores. | Generally undisturbed forest have a high number of carnivores species as eastern cougar, black bear, fisher, bobcat, wolf and fox. Three categories are purposed: control/normal (≥ 6 species), intermediate (3-5 species), low (<3 species). |
| | 10. Forest area. | This descriptor is very important. Disturbed forests are generally fragmented in woodlots. In order to maintain an avian community typical of undisturbed stands necessitates 75 ha of continuous forest and 100,000 ha for complete assemblage of mammals. Three categories are proposed: control/normal (>$10^5$ ha), intermediate ($10^2$ -$10^5$ ha), low (<$10^2$ha). |

humanity at different times and in different parts of the world has always been followed by a divergence by the processes of the ecological systems. We can learn an important lesson from the Everglades. This system has been managed in different ways according to the different crises that have created the conditions for new management eras (Figure 7.11) (Gunderson et al. 1995). The inclusion of the spatial dimension in ecological conservation means taking into account variables often neglected, and the spatial effects that can have consequences over time. This is the case of the hypothesis presented by Tilman et al. (1994) on the behavior of species extinction during habitat destruction. Also the more a habitat is already fragmented, the higher the number of extinctions by added destruction. This effect, which appears generations after fragmentation, represents a debt or the future costs of current habitat destruction (Figure 7.12).

## 7.9 APPLICATION OF THE "FULL" VERSUS "EMPTY" WORLD HYPOTHESIS TO LANDSCAPE MANAGEMENT

The future of the rural lndscape largely depends on our view of the world. In order to maintain strict and everyday contact with the natural processes it is necessary to change our ideas about nature and human development.

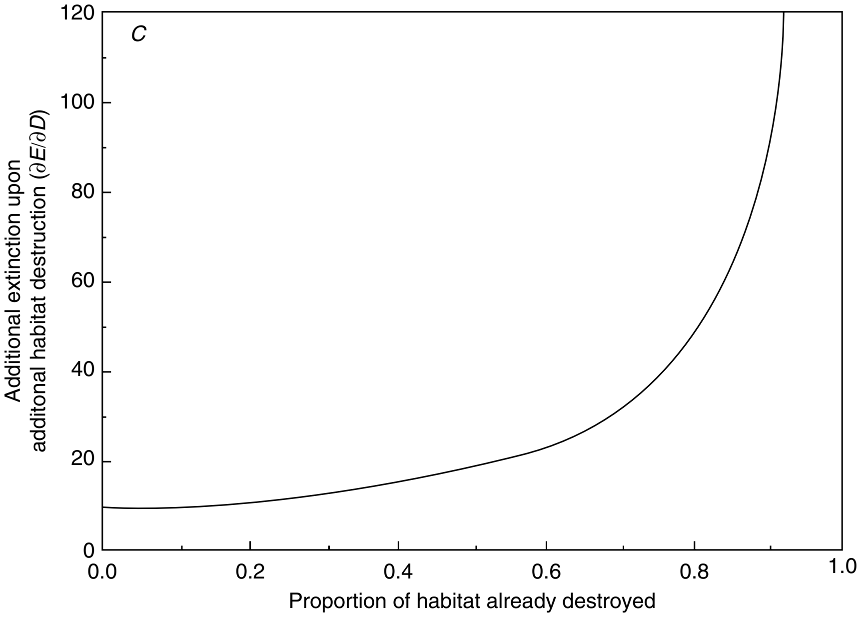

*Figure 7-12*. Representation of the pattern of additional extinction in habitats already destroyed (from Tilman et al. 1994, with permission).

The “Full” world hypothesis (Farina et al. 2003) in which natural and human dynamics are strictly connected in terms of reuse and multiple use of resources was suggested by Beisman (1997), who recommends a nature-compliant agriculture. Such an approach recognizes the importance of not doing intensive agro-production and nature conservation separately and including cultural components of the landscapes (Naveh 1994, 1995b, 1998).

## 7.10 SPATIALLY EXPLICIT MODELING APPROACH APPLIED TO ANIMAL DYNAMICS

The recent use of models that have spatially explicit characters powered by computer-simulated routines have opened new perspectives to land management (Heleno & dos Santos 1998; Gergel 2004; Gustafson et al. 2004, Lawler et al. 2004). In fact, such models can simulate every condition that a focal species has to experience to maintain life functions. In particular, such models can also be applied to future scenarios to control invading species like the North American *Sciurus carolinensis* in northern Italy (Lurz et al. 2001) as well as for endangered species.

Ecological models for landscape planning are frequently used in problematic areas like the Mediterranean basin (Zavala & Burkey 1997). Landscape patterns have been used as habitat predictors of cavity-nesting birds in the Uinta Mountains of Utha (USA) by Lawler & Edwards (2002). Similar conclusions are presented by Estades (2001), modeling breeding-habitat patch size and matrix quality. From that simulation, it appeared that larger patches support a higher density of breeders. But after an increase of food availability in the surrounding matrix, this effect diminishes. The best scenario is represented by extended foraging areas around large patches. This result has important implications for species conservation when remnant patches cannot be improved, like the old-growth fragments in timber areas. Supplying additional foraging sites like what happens when reforestation occurs around old-growth fragments, large and food generalist species can be advantageous. This could be the case of spotted owls (*Strix occidentalis*), which can also forage in secondary forests if these are surrounding old-growth stands in which they can breed and roost.

## 7.11 THE LANDSCAPE SPECIES APPROACH

Recently, Coppolillo et al. (2004) have proposed a rationale to select a focal species that can adapt to describe landscape features: area requirement, heterogeneity, ecological funtion, vulnerability and socioeconomic relevance (Figure 7.13). Sanderson et al. (2002) have defined a landscape species by “their use of

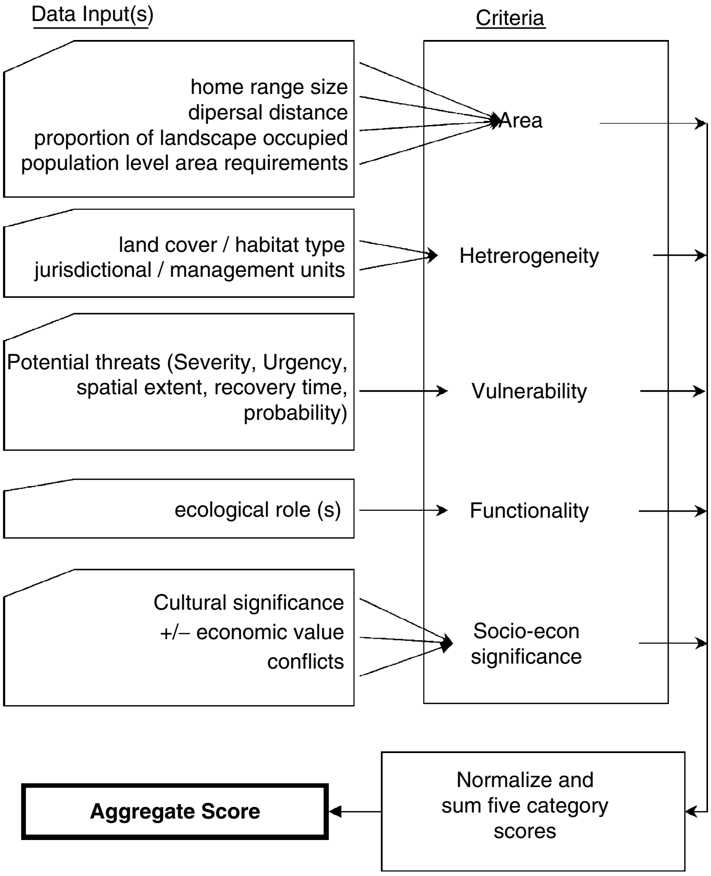

*Figure 7-13*. Data introduced into the model to select the five criteria for a landscape species candidate (from Coppolillo et al 2004, with permission).

large, ecologically diverse areas and their impacts on the structure and function of natural ecosystems.... their requirements in time and space make them particularly susceptible to human alteration and use of wild landscapes”. This method seems a good compromise between a focal-species approach and a human landscape approach.

It is not for all species that the resources are restricted to the breeding area and landscape complementation seems a necessary strategy for preserving populations. This is particularly evident in frogs, as discussed by Pope et al. (2000) that alerts us about the neccesity to consider not only the metapopulation structure to conserve leopard frogs (*Rana pipiens*) populations, but that the surrounding landscape is also important for rescue and recolonization.

## 7.12 URBAN LANDSCAPE: GREENWAYS AND SAFETY

Greenways have been proved to increase biodiversity and recreational opportunities in urban and suburban areas. Generally, greenways are the result of an active policy to recreate ecosystem services in urban areas. Despite the ecological benefits that greenways assure to the entire urban landscape, some problems are awaiting solution. In particular, the greenways pose problems of safety for women, aged people, children and the disabled. These categories feel unsafe in such fragments of the natural environment. And, as argued by Luymes & Tamminga (1995), many municipalities are reluctant to encourage the planning of green spaces. These authors emphasize the theory of prospect and refuge (Appleton 1996) in order to produce greenways that are perceived by people in a safe way. The criteria utilized were in response to the following requirements: visibility of others, visibility by others, choice and control, environmental awareness and legibility, solitude without isolation. These principles can be realized according to the different standards selected at the national level. Healthy places and people's confidence in the environmental context are two faces of the same coin.

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Chapter 8

# METHODS IN LANDSCAPE ECOLOGY

## 8.1 INTRODUCTION

This chapter represents an attempt to describe, using different approaches, the geometrical attributes of landscapes. The argument remains extremely difficult to reduce to a simple presentation due to the pletora of methods used by authors in very different circumstances, as argued by Hargis et al. (1997). This chapter would not be complete with only books devoted specifically to landscape ecology methods (Turner & Gardner 1991; McGarigal & Marks 1995, Gergel & Turner 2002), but the aim is to introduce and orient the reader toward the main quantitative approaches to measuring landscape features. Consequently, it is important to immediately clarify that the study of the landscape requires metrics but also additional tools like Databases, Spatial Statistics, Geographic Information Systems, Remote Sensing Techniques and Global Positioning Systems, that are used in many other circumstances. In fact, these methodologies are applied in geology, geography, navigation, agronomy, climatic economics and social sciences, forecasting, epidemology, etc.

The chapter has been divided into three main parts: landscape metrics, Geographic Information Systems, Global Positioning System. The two last arguments are described in terms of their applications to landscape studies without entering into the technical details due to the scope of the book. Actually, several public dominion and commercial software and associated userguides and manuals are available either for landscape metrics (FRAGSTAT, (McGarigal & Marks 1995), LEAPII (Perrera et al. 1997), Patch Analyst (Elkie et al. (1999), APACK (Mladenoff & DeZonia (2000)), for GIS

*Table 8-1*. Indices calculated to analyze the landscape using the program FRAGSTATS (McGarigal & Marks 1995).

| | |
|---|---|
| Total Area (ha) | Mean Core Area 1 (ha) |
| Largest Patch Index(%) | Core Area Standard Deviation 1 (ha) |
| Number of patches | Core Area Coefficient of Variation 1 (%) |
| Patch Density (#/100 ha) | Mean Core Area 2 (ha) |
| Mean Patch Size (ha) | Core Area Standard Deviation 2 (ha) |
| Patch Size Standard Dev (ha) | Core Area Coefficient of Variation 2 (%) |
| Patch Size Coefficient of Variation (%) | Total Core Area Index (%) |
| Total Edge (m) | Mean Core Area Index (%) |
| Edge Density (m/ha) | Mean Nearest Neighbor (m) |
| Contrast-Weight Edge Density (m/ha) | Nearest Neighbor Standard Deviation (m) |
| Total Edge Contrast Index (%) | Nearest Neighbor Coefficient of Variation (%) |
| Mean Edge Contrast Index (%) | Mean Proximity Index |
| Area-Weighted Mean Edge Contrast (%) | Shannon's Diversity Index |
| Landscape Shape Index | Simpson's Diversity Index |
| Mean Shape Index | Modified Simpson's Diversity Index |
| Area-Weighted Mean Shape Index | Patch Richness |
| Double Log Fractal Dimension | Patch Richness Density (#/100 ha) |
| Mean Patch Fractal Dimension | Relative Patch Richness (%) |
| Area-Weighted Mean Fractal Dimension | Shannon's Evenness Index |
| Total Core Area (ha) | Simpson's Evenness Index |
| Number of Core Areas: | Modified Simpson's Evenness Index |
| Core Area Density (#/100 ha) | Interspersion/Juxtaposition Index |

(MapInfo, Arcwiev, GRASS, etc.) and GPS (Trimble Navigation 1994, Farrell & Barth1999) as well (see Table 8.1).

Routines and practical examples are provided to guide you across several possibilities to quantify many, but not all the attributes of landscapes. In fact, the landscape approach may be so diverse that it is not possible to comprehensively review all methods and indicate standard methodologies. Many of those have been borrowed from geobotanics, animal population analysis, behaviour ecology, etc. and the need to integrate environmental information, like topography, into landscape analysis, as emphasized by Dorner et al. (2002).

There are at least four methodological approaches to studying landscape metrics: numerical analysis, spatial analysis, multiscalar analysis and finally, spatial modeling analysis (Figure 8.1).

## 8.2 METRICS IN LANDSCAPE ECOLOGY

The spatial elaboration of data is a central affair in landscape ecology and for this reason we will dedicate a large amount of space to the argument. Many techniques have been borrowed mainly from spatial statistics or geosta-

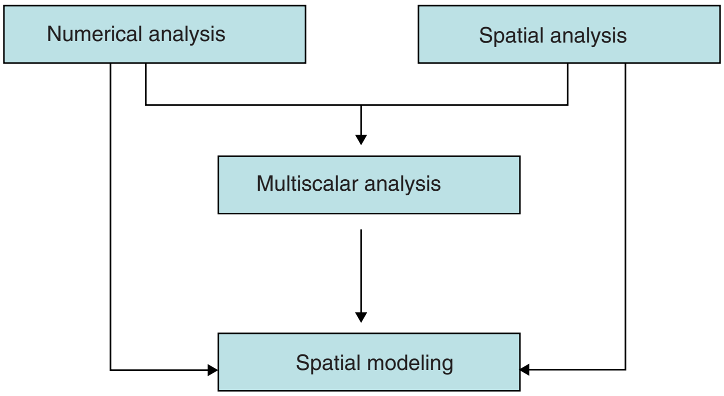


*Figure 8-1*. The principal approaches to landscape metrics (from Farina 2000, with permission).

tistics, for image analysis and fractal geometry. Euclidean and non-Euclidean geometry are often combined to analyze the complexity of spatial processes and patterns across temporal and spatial scales (Jenerette & Wu 2001, Lausch & Herzog, 2002). Several metrics to describe landscape patterns are available today, but often the metrics sensitivity is not fully validated, as argued by Trani & Giles (1999), (see also Riitters et al. 1995; Hargis et al. 1998; Bartel 2000; McAlpine & Eyre 2002; Tischendorf 2001; Baldwin et al. 2004; Li & Wu 2004).

Landscape analysis can be performed on at least at four levels of spatial resolution: individual, patch, mosaic and landscape (Figure 8.2). We target an individual species (plants, animals) or a distinct object (houses, bridges, etc.). Patch resolution means that the analysis is restricted to a focal spatial unit like an urban garden, a forest gap or a woodlot. Mosaic resolution represents a window selected for some reason, for instance, by a sampling technique, in which two or more patches are included. Finally, the landscape is a mosaic of patches delimited in extension by significant natural or human-perceived coherences. In

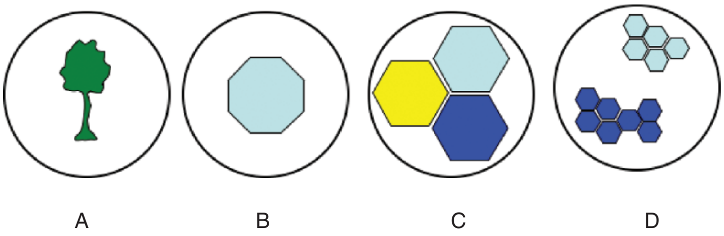


*Figure 8-2*. Metrics in landscape ecology can be applied at individual (A), patch (B), mosaic (C) and finally, at landscape scales (D) (from Farina 2001, with permission).

this last case, more complicated analyses are necessary to explore the complexity contained within the landscape.

### 8.2.1 Non-spatial metrics

This section will describe some numerical indexes that have a very broad utilization in ecology and biology as well. Specifically, Richness, Diversity and Evenness are very useful to describe non spatial attributes of the landscape.

*Richness*
It is the simplest attribute measurable in a collection. It is defined as the number (S) of different objects (organisms, patches, etc.) ($n_i$) present in a collection.

$$S = \sum n_i \tag{1}$$

*Diversity*

This attribute describes the uncertainty by which we can encounter a new object, sampling a collection at random and it is the combination of richness and evenness. It does not exist as a universal index, but according to the typology of the collection, some are more efficient than others in tracking the information. We present the Simpson and Shannon indices (See Table 8.2). The first index is particularly sensitive to the most abundant species and the second to the rarest.

*Simpson Diversity* (Simpson 1949)

$$\lambda = \sum_{i=1}^{S} pi^2 \tag{2}$$

*Table 8-2*. Indices of the spatial arrangement of the mosaic (from a subset of 8x8 km, see Fig. 8.7): L(r) lacunarity r=2x2, pi=relative abundance, Diversity (Shannon Diversity)=1.31, Simpson Diversity=3.03, Dominance=.464 .

*Contagion 2.28.*

| *Land cover code* | *abundance* | *pi* | *pi*$^{x}$*log pi* | *L(r)* | $p_i^2$ |
|---|---|---|---|---|---|
| 1 | 799 | 0.499 | -0.347 | 1.52 | .249 |
| 2 | 34 | 0.021 | -0.082 | 20 | .000 |
| 3 | 399 | 0.249 | -0.346 | 2.34 | .062 |
| 4 | 125 | 0.078 | -0.199 | 5.86 | .006 |
| 5 | 4 | 0.003 | -0.015 | 138 | .000 |
| 6 | 16 | 0.010 | -0.046 | 48 | .000 |
| 7 | 223 | 0.139 | -0.275 | 4.08 | .019 |
| Tot. | 1600 | 1 | -1.31 |  | .33 |

where S is the number of categories, pi is the relative abundance. pi=ni/N where ni is the abundance of category i and N is the total abundance.

*Shannon Diversity*

The variety and relative abundance of objects can be estimated using the Shannon Index (Shannon & Weaver 1949)

$$H' = \sum_{i=1}^{S} (pi \ln pi) \tag{3}$$

where pi is the relative importance of the category i.

## Evenness

This attribute describes the deviance between a maximum equipartition of the objects into a collection (when every category has the same importance) and the distribution observed. Three indices are proposed:

*Pielou Evenness* (Pielou 1975, 1977)

$$E1 = \frac{H'}{\ln(S)} \tag{4}$$

*Sheldon Evenness* (Sheldon 1969)

$$E2 = \frac{e^{H'}}{S} \tag{5}$$

*Dominance* (O'Neill et al. 1988)

This index, related to the Shannon index, measures the value of dominance of one land cover over the others

$$D = \text{In}\,n - H' \tag{6}$$

where H'=–∑ pi ln pi where pi is the proportion of the grid cells on the landscape for the land use i is selected. n is the number of land use categories.

D is close to 0 when the land cover types present an equi-abundance and is close to 1 when most of the land cover type belongs to one type.

*Heip Evenness* (Heip 1974)

$$E3 = \frac{e^{H'} - 1}{S - 1} \tag{7}$$

where H′ is the Shannon diversity and S is the richness.

*Hill Evenness* (Hill 1973)

$$E4 = \frac{(1/\lambda) - 1}{e^{H'}} \tag{8}$$

where λ is the Simpson diversity and H' the Shannon diversity.

## 8.2.2 Spatial metrics

The metrics described in this section measure the spatial arrangement of objects. Spatial configuration is recognized as important to assessing habitat suitability. In fact, landscapes with different habitat configurations are expected to be used differently by species (McIntyre & Wiens 2000).

### *Relative Patchiness*

$$RP = 100 \sum\sum \frac{EijDij}{Nb} \tag{9}$$

n is the total number of patch types in a mosaic, Eij is the number of edges between patch types i and j, Dij is the dissimilarity value for patch types i and j, and Nb is the total number of edges of pixels (each pixel has four edges).

This index measures the contrast of neighboring patch types in a landscape mosaic. See Romme (1982) for an example of its application.

### *Entropy*

This index measures the disorder of pixels for each category.

$$ENT = -\sum\sum Pij \ln Pij \tag{10}$$

Pij is the probability of a grid point of land use, i is adjacent to a grid point of land use j. Pij represents the probability that land use type i is adjacent to cells of type j. The Pij value is calculated by dividing the number of cells of type i that are adjacent to j by the total number of cells of type i present in the matrix. Pij=Nij/Ni, where Nij is the number of adjacencies between pixels of patch type i and j. Ni is the total number of cells of type i. Nij=Ni. Then Pij=1 (O'Neill et al. 1988, Turner et al. 1989, Li & Reynolds 1993).

### *Contagion*

This index derives from information theoretical measures (Shannon & Weaver 1948) and measures the degree of clumping. It represents the deviation of the entropy measure from its possible maximum value

$$C = 2 \ln m - ENT \tag{11}$$

where $ENT = -\sum\sum Pij \ln (Pij)$ (see equation 10).

This index measures whether cells are aggregated or clumped.
2 ln m represents the maximum possible probability of adjacency. If the value of Contagion is high, it means that contiguous patches are found in the landscape. If the value is low, the landscape is composed of small patches.

## Relative contagion

This index, proposed by Li & Reynolds (1993), utilizes the same components of the formula of point l, but the Entropy is divided by the Max Entropy, so that the RC varies between 0 and 1 and represents an evenness index.

$$RC = \frac{1 - ENT}{2 1\mathrm{n} m} \tag{12}$$

## Beta Organization Index

This index, proposed by Ernoult et al. (2003), measures the degree of deviation by which the spatial distribution of a landscape entity (e.g., the meadow land cover) is independent from the distribution of another (e.g., soil type).

$$R_S(L) = \frac{H(L) + H(S) - H(L \times S)}{H(L)} \tag{13}$$

where H(L)=–Σ(i land use)pi log pi, where pi is the probability to find i land use in the study area.

H(S) is the marginal entropy of the (geographical or biological) character for which we try to find a spatial concordance H(S)=-Σ(i geographical or biological character)pi log pi

H(L.S)= -Σ(i land use)(Σ(j soil types)pij log pij)

This index reaches the value of 1 when all land uses areas located according to specific environmental niches and, consequently, the co-occurence is maximum, for instance, between land use and soil character.

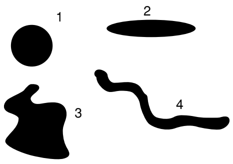
### 8.2.2.1 Patch shape metrics

Many indices have been formulated to measure patch shape, especially in a geographical context. We have selected some indices frequently used in direct landscape analysis (see Table 8.3). These indices have to be adopted and used with caution because often the precise ecological relationship with the process investigated is not so easily found. In any case, the approach of the study of patch shape is important for the consequences that patch regularity/irregularity has on organisms. We assume the circle as a regular patch, the more a patch is irregular and the more edges and less interior (core) area are available (Figure 8.3). Irregular patches probably have more heterogeneous processes than regular ones. Habitat suitability, predation risk, microclimatic stresses are some of the direct consequences of an irregular patch (Figure 8.4). This, of course, is important for some species but not for all.

Six indices calculating patch shape are described:

*Table 8-3*. Some patch shape measures applied to four types of patches (1,2,3,4)

#patch= Patch Identifier
S= Area (Patch size, in pixel)
L= Perimeter (Patch edge, in pixel)
S/L = Ratio Area/Perimeter
CORR (Corrected Perimeter-Area) = .282*L/√S
RCC (Related Circumscribing Circle) = 2*(S/π)1/2)/longest-axis
Long-Axis (Longest Axis)
Data have been processed using the routine basic MPC of Box 6.1



| *#patch* | *S* | *L* | *S/L* | *CORR* | *RCC* | *Long-Axis* |
|---|---|---|---|---|---|---|
| 1 | 4838 | 259.52 | .054 | 1.052 | .994 | 79.010 |
| 2 | 4235 | 356.27 | .084 | 1.544 | .451 | 162.720 |
| 3 | 11055 | 521.24 | .047 | 1.398 | .867 | 136.900 |
| 4 | 5639 | 662.32 | .117 | 2.487 | .448 | 189.090 |

## *Perimeter-Area Ratio*

The perimeter of each patch is simply divided by its area

$$\frac{L}{S} \tag{13}$$

L = Perimeter, S= Area

This index varies according to the size of the patch even if the shape is constant. See Buechner (1987) for an application of a field study of mammal dispersion.

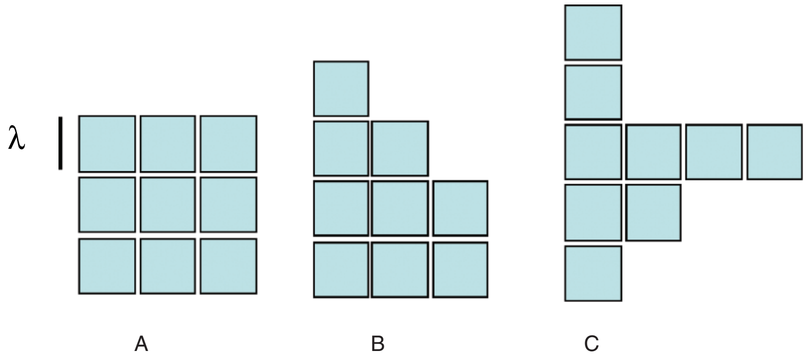


*Figure 8-3*. Patch shape remains one of the most important morphological attributes to measure in a landscape. It is easy to recognize an increase of the perimeter moving from a regular patch A (λx9) to B (λx14) until the most irregular C (λx18). Consequently, changes in the ratio between area and perimeter modify patch functioning and habitat quality.

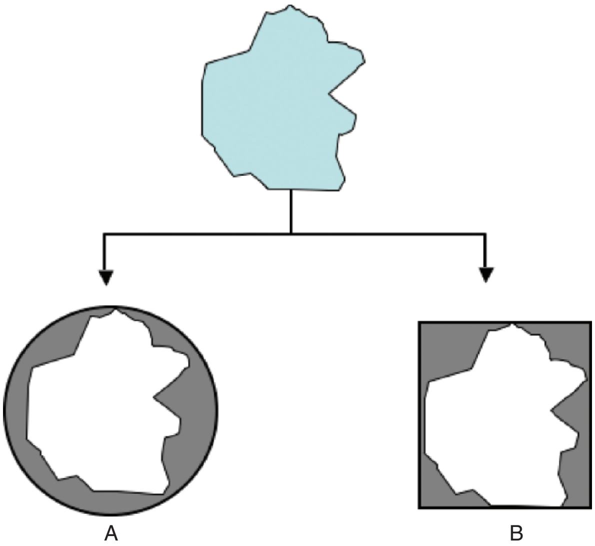


*Figure 8-4*. Some indices that describe patch shape are based on the differences between the shape of a patch and a circle or a quadrat that has aproximately the same surface area.

## *Area-Perimeter Ratio*

Three indices are available:

$$\gamma 1 = \frac{2\sqrt{\pi A}}{P} \tag{14}$$

$$\gamma 2 = \frac{4\sqrt{A}}{P} \tag{15}$$

$$\gamma 3 = \frac{A}{P^2} \tag{16}$$

$\gamma 2$ and $\gamma 3$ for patches represented in a raster format.

## *Corrected Perimeter-Area (CPA)*

This index is corrected for solving the size problems of the index no. 1 and varies between 0.0, a perfect circle to infinity for an infinitely long and narrow shape.

$$CPA = \frac{.282 \times L}{\sqrt{S}} \tag{17}$$

L= perimeter, S=Area

### *Related Circumscribing Circle (RCC)*

This index compares the patch size with the size of a circle that can circumscribe the patch.

$$RCC = \frac{2 \times (area/\pi)^{\frac{1}{2}}}{longest - axis} \tag{18}$$

This index varies between 0.0 to 1.0 as the shape of the patch approaches a circle.

### *Shape Index S1 (Hulshoff 1995)*

$$S1 = \frac{1}{Ni}\sum\frac{Li}{Si} \tag{19}$$

where Ni is the number of patches of category i in a map, Li is the perimeter and Si the area of each patch in category i. A high value of this index indicates the presence of many patches with small interiors.

### *Shape Index S2 (Hulshoff 1995)*

This index measures the isodiametric attributes of patches

$$S2 = \frac{1}{Ni}\sum\frac{Li}{4\sqrt{Si}} \tag{20}$$

where Ni is the number of patches of category i, Li is the perimeter and Si is the size of each patch in the category. The farther S2 is from 1, the more the patches deviate from an isodiametric shape.

### *Fractal Dimension D (see more on fractals in chapter 8.3)*

The complexity of a path shape can be measured by regressing the log of the patch perimeter (L) with the log of the patch size (S).

$$\mathbf{D = 2s} \tag{21}$$

where s is the slope of the regression

### *Patch Density*

$$PD = \frac{ni}{A} \tag{22}$$

where ni represents the number of patches of category i and A is total area of the matrix.

### *Mean Patch Size*

$$MPS = \frac{\sum_{j=1}^{n} aij}{ni} \tag{23}$$

where ni is the number of patches of category i and aij is the area of each patch of category i.

### Largest Patch Size

$$LPS = \frac{Max(aij)}{A}100 \tag{24}$$

### Border Length

$$BL = \sum_{k=1}^{m} eik \tag{25}$$

### Border Contrast

$$BC = \frac{\sum_{k=1}^{m}(pijk \times dik)}{pij}100 \tag{26}$$

### Total Core Area

$$TCA = \sum_{j=1}^{n} aij^{c} \tag{27}$$

where c is the buffer size.

### Relative Core Area

$$RCA = \frac{\sum_{j=1}^{n} aij^{c}}{\sum_{i=1}^{n} aij} \tag{28}$$

### 8.2.2.2 Distance metrics

Distance of a patch or a group of patches from others is an important parameter in mosaic analysis.

Distance means energy loss for moving, increasing predatory risk and decreasing transportation by vectors, etc. (van Dorp & Opdam 1987). Distance also means connectedness and connectivity.

The calculation of distance can be done according to a combination of possibilities, as discussed in detail by Baker & Cai (1992) and summarized in Table 8.4. The measurement of distances can be done according a selection of possibilities: 1. from each patch to all the adjacent neighbors of each patch. 2. from a patch to all others of the same group, 3. from each patch to the single nearest patch of a different group, 4. from a patch of a specific group to another patch of a specific group (Figure . 8.5 and Table 8.6).

The degree of isolation of the patches is measured with the proximity index PX (Gustafson & Parker 1992).

*Table 8-4*. Measures utilized for calculating distances (gp=attribute group) (from Baker & Cai 1992, with permission).

| *Measures:* |
|---|
| Mean distance |
| Standard deviation distance |
| Mean distance by gp |
| Standard deviation distance by gp |
| Number of distances in each distance class |
| Number of distances in each distance class by gp |

*Table 8-5*. Measures of pixel attribute, patch size, shape, fractal dimension and perimeter (from Baker & Cai 1992, with permission).

| *Attribute:* |
|---|
| Mean pixel attribute |
| Standard deviation pixel attribute |
| Mean patch attribute |
| Standard deviation patch attribute |
| Cover by gp |
| Density by gp |
| *Size:* |
| Mean patch size |
| Standard deviation size |
| Mean patch size by gp |
| Standard deviation size by gp |
| Number in each size class |
| Number in each size class by gp |
| *Shape:* |
| Indices: |
| Corrected perimeter/area |
| Perimeter/area |
| Related circumscribing circle |
| Measures: |
| Mean patch shape |
| Standard deviation shape |
| Mean patch shape by gp |
| Standard deviation shape by gp |
| Number in each shape class |
| Number in each shape class by gp |
| *Fractal dimension:* |
| Perimeter=area fractal dimension |
| *Perimeter:* |
| Sum of perimeters |
| Sum of perimeters by gp |
| Mean perimeter length |
| Mean perimeter length by gp |
| Standard deviation perimeter length |
| Standard deviation perimeter length by gp |

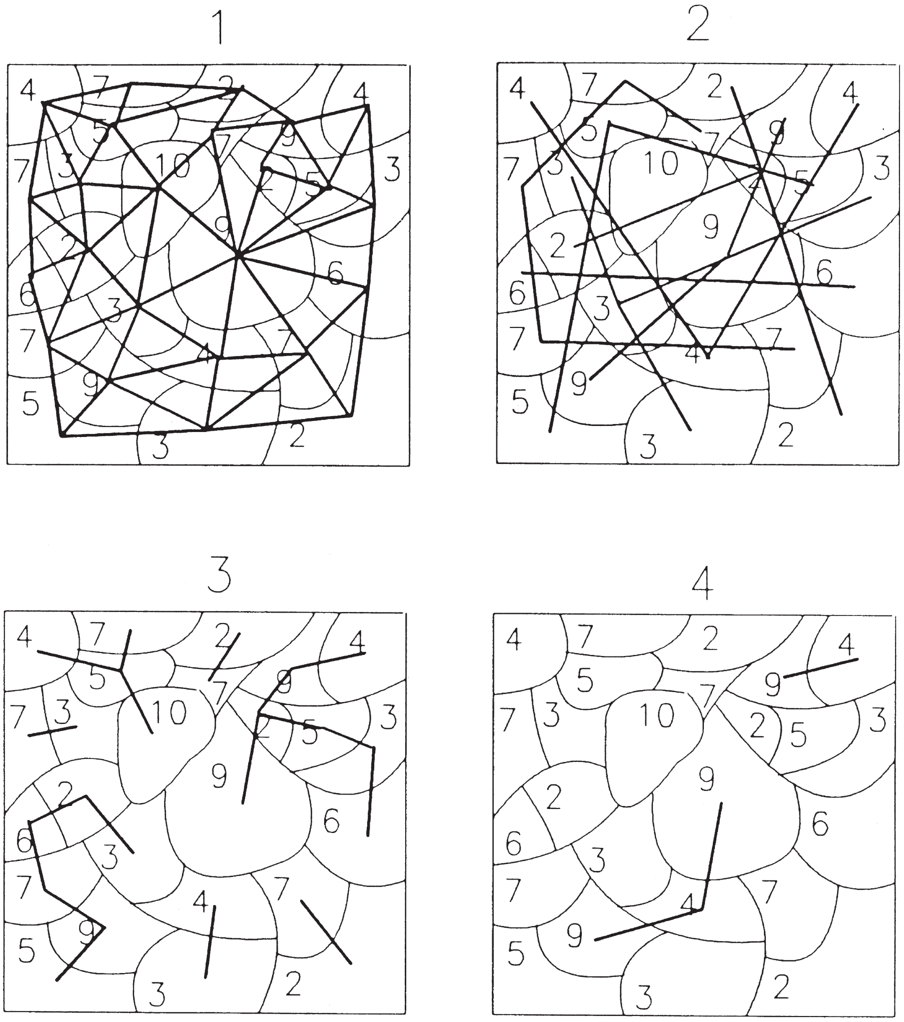


*Figure 8-5*. Four possible methods to measure distance. 1,2,3,4 see text for explanation (from Baker & Cai 1992, with permission).

$$PX = \sum \frac{Sk}{nK} \tag{29}$$

where Sk is the area of the patch and nk is the nearest neighbor distance of patch K. This index can be scaled as a proportion of the maximum value of PX, then PXs=PX/PXmax where PXmax=E/n, E is half of the total area of landscape separated by the minimum possible n.

Table 8-6. Value of co-occurrence frequency matrix (A1, B1, C1) and the co-occurrence matrix of probability derived by A1, B1, C1 matrix, respectively, dividing the frequencies by the total number of co-occurrences (from Musick & Grover 1991, modified, with permission).

| *A1* | 21 | 22 | 23 | 24 |
|---|---|---|---|---|
| 21 | 4 | 2 | 0 | 0 |
| 22 | 2 | 0 | 0 | 1 |
| 23 | 0 | 0 | 0 | 1 |
| 24 | 0 | 1 | 1 | 0 |

| *B1* | 21 | 22 | 23 | 24 |
|---|---|---|---|---|
| 21 | 10 | 7 | 1 | 1 |
| 22 | 7 | 2 | 1 | 3 |
| 23 | 1 | 1 | 0 | 1 |
| 24 | 1 | 3 | 1 | 0 |

| *C1* | 21 | 22 | 23 | 24 |
|---|---|---|---|---|
| 21 | 6 | 8 | 0 | 2 |
| 22 | 8 | 2 | 2 | 2 |
| 23 | 0 | 2 | 0 | 2 |
| 24 | 2 | 2 | 2 | 0 |

| *A2* | 21 | 22 | 23 | 24 |
|---|---|---|---|---|
| 21 | .333 | .1.67 | 0 | 0 |
| 22 | .167 | 0 | 0 | .083 |
| 23 | 0 | 0 | 0 | .083 |
| 24 | 0 | .083 | .083 | 0 |

| *B2* | 21 | 22 | 23 | 24 |
|---|---|---|---|---|
| 21 | .250 | .175 | .025 | .025 |
| 22 | .175 | .050 | .025 | .075 |
| 23 | .025 | .025 | 0 | .025 |
| 24 | .025 | .075 | .025 | 0 |

| *C2* | 21 | 22 | 23 | 24 |
|---|---|---|---|---|
| 21 | .150 | .200 | 0 | .050 |
| 22 | .200 | .050 | .050 | .050 |
| 23 | 0 | .050 | 0 | .050 |
| 24 | .050 | .050 | .050 | 0 |

PXs cannot be used to compare two landscapes of different extents because PXmax changes according to the landscape extent.

### *8.2.2.3 Texture metrics*

The texture measures are adopted to analyze patterns of brightness variations within an image (see Musick & Grover 1991; Haralick et al. 1973) (Table 8.5).

These measures can be used profitably in landscape ecology to analyze the complexity of the mosaic and the contrast among patches.

The spatial co-occurrence probability p(i,j,d,q) where a pixel or a cell of type i is separated by a pixel or a cell of type j by the distance d according to an angle direction q that may be 0° horizontal, 45° right diagonal, 90° vertical, 135° left diagonal. The comparison involves two reciprocal co-occurrences and the matrix produced is symmetrical. Figure 8.6 presents three examples of analysis of co-occurrences.

Two indices of homogeneity may be used in the analysis of landscape texture: the Angular Second Moment (ASM) and the Inverse Difference Moment (IDM).

## *Angular Second Moment*

ASM is the sum of co-occurrences probabilities:

$$\mathrm{ASM}=\Sigma\Sigma[p(i,j)]^2 \qquad (20)$$

where p(i, j) is the relative abundance of the cells i that are in adjacency with the cells j. p(i, j)= n(i, j)/tot, where n(i, j) is the number of occurrences of cell i adjacent to cell j. tot=ΣΣ n(i, j). See Box 2 for routine in Basic to calculate ASM.

ASM increases with mosaic homogeneity because the co-occurrence of identical values has a strong influence on this index. In homogeneous patches, the co-occurrence of cells with identical value are dominant and the squared probabilities enhance this value. ASM has the value 1 when all co-occurrences are identical, but this index is not sensitive to the magnitude of difference between cells of different value.

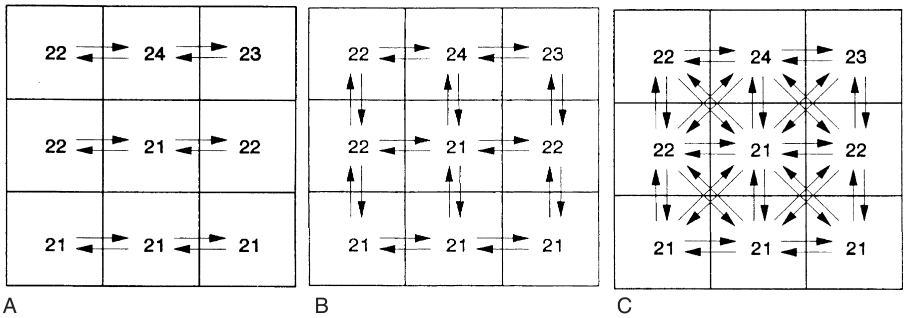


*Figure 8-6*. Three possibilities to calculate the co-occurrence probability p(i,j,d,q) between cells or pixels of a matrix. The number in the cells indicates the type of attribute, maybe a land-cover or vegetation or color attribute. In case A the co-occurrences have been measured only along the horizontal axis (q=0°), in B according to the four perpendicular directions (q=0°,90°) and C in all directions(q=0°,45°,90°,135°) at a distance d=1 (from Musick & Grover 1991, modified, with permission).

### *Inverse Difference Moment*

$$IDM=\Sigma\Sigma[\ 1/1+(i-j)2\ ]\ p(i,j) \tag{21}$$

This index measures the co-occurrences weighted according to the difference between values of i and j. The index has maximum value of 1 when all cells or pixels are identical. To be usefully applicable in land analysis the differences of value of i and j must have some significance (intensity or interval type data). In the example in Figure 8.7 the values of the landscape matrix from 1 to 7 have been ranked according to biomass cover. (1, dense beech forest to 7, rock outcrops).

### *Contrast*

This index measures the contrast present in the landscape.

$$CON=[\ (i-j)2\ {*}Pij \tag{22}$$

### *Temporal Change*

This index measures the change in the surface of a patch timed over years

$$C=((pk2-pk1)/(t2-t1))/n \tag{23}$$

where pk2 is the surface of category k in time 2 and pk1 the same category in time 1, t2 and t1 are respectively the date of the time-lag.

Figures 8.7, 8.8, 8.9 and Tables 8.7 and 8.8 describe an example of the application of spatial indices to the study of landscape mosaics.

### *Lacunarity*

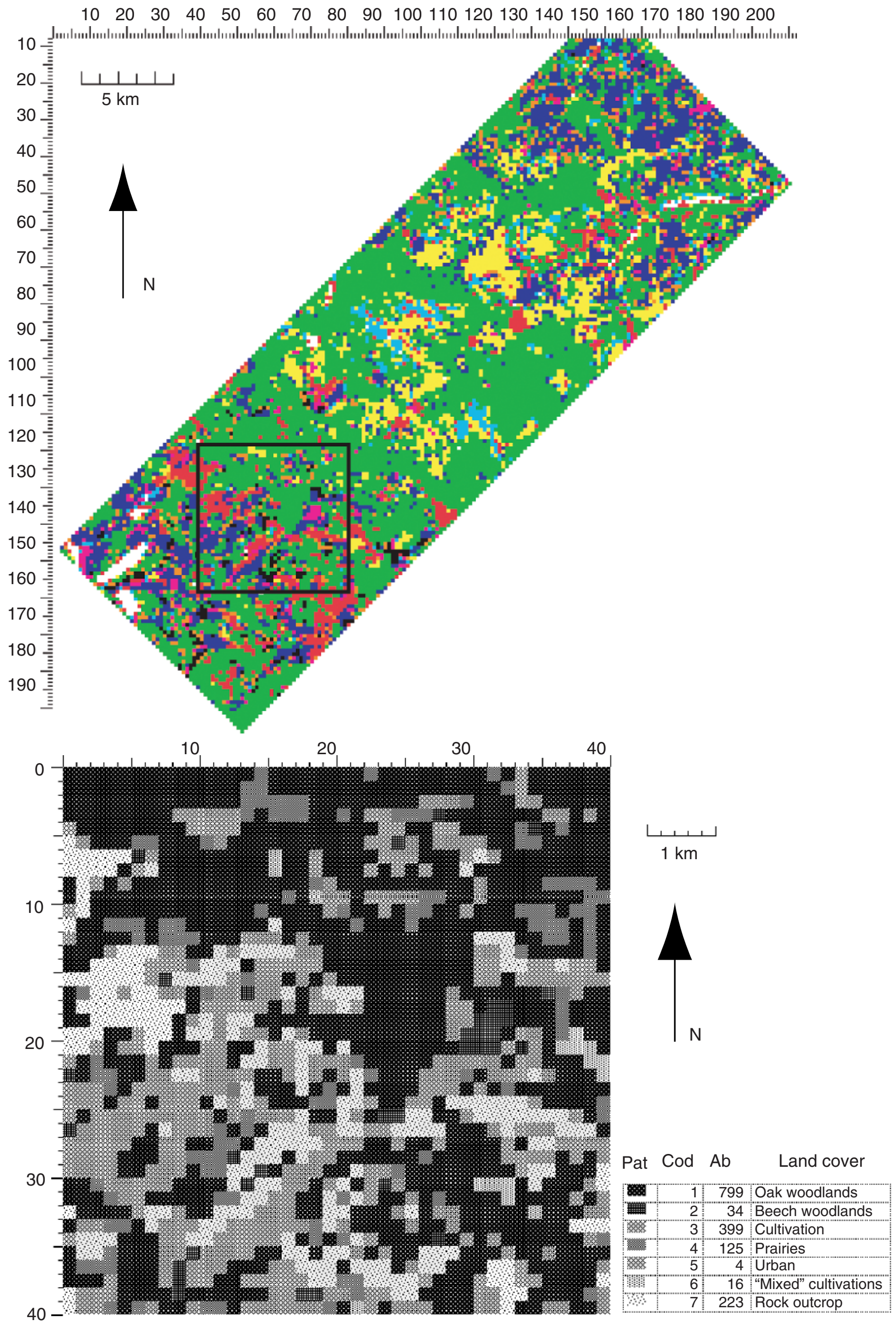
Deterministic fractals with identical dimensions can have a different appearance, as in the case of Cantor dusts with a difference of 0.5.

Mandelbrot called the distribution of gap size as “lacunarity” (Mandelbrot 1983). Lacunarity measures the distribution of gaps in a fractal figure. An object with a low lacunarity is invariant when translating, on the other hand, an object with a heterogeneous gap size is not translationally invariant. But we have to consider that the invariance is scale dependent. An object invariant at a small scale may be heterogeneous at a broad scale and *vice-versa*.

Translational invariance is not synonymous with self-similarity.

Lacunarity has advantages when compared with other indices of landscape structure (Plotnick et al. 1993):

The algorithm is relatively simple.
The gliding box algorithm samples the map in sufficient ways to quantify change in contagion and self-similarity with scale.
The results are not sensitive to a boundary map. This analysis can be used for very sparse data.



| Pat | Cod | Ab | Land cover |
|---|---|---|---|
| ■ | 1 | 799 | Oak woodlands |
| ■ | 2 | 34 | Beech woodlands |
| ▨ | 3 | 399 | Cultivation |
| ▨ | 4 | 125 | Prairies |
| ▨ | 5 | 4 | Urban |
| ▨ | 6 | 16 | "Mixed" cultivations |
| ▨ | 7 | 223 | Rock outcrop |

*Figure 8-7*. Subset of 8x8 km, 200x200 m cells, of a GIS ( Routine MacGIS (Hulse & Larsen 1989)), across the northern Apennines (from Nardelli 1995). The mosaic is composed of 7 mainland covers. Pat=Graphic Pattern, Cod= Land cover code, AB= Number of cells.

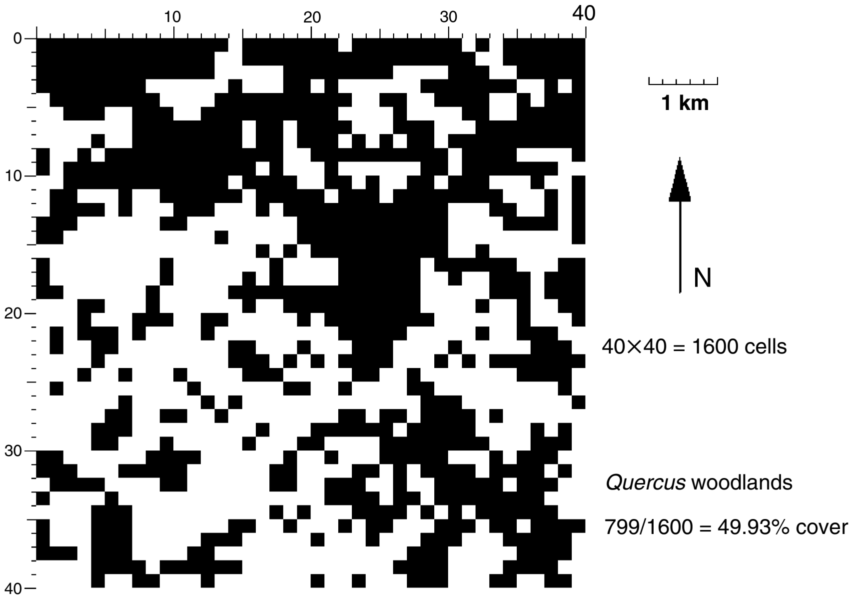


*Figure 8-8*. Example of landscape analysis using a single land cover, in this case the oak woodlands cover (source from Nardelli 1995) see also Fig. 8.7 for the complete mosaic. From this image it is possible to measure:
No. Patch, Area, Perimeter, Shannon diversity of patch size, Shannon diversity of patch edge, Max., Min., Patch size and Patch edge.

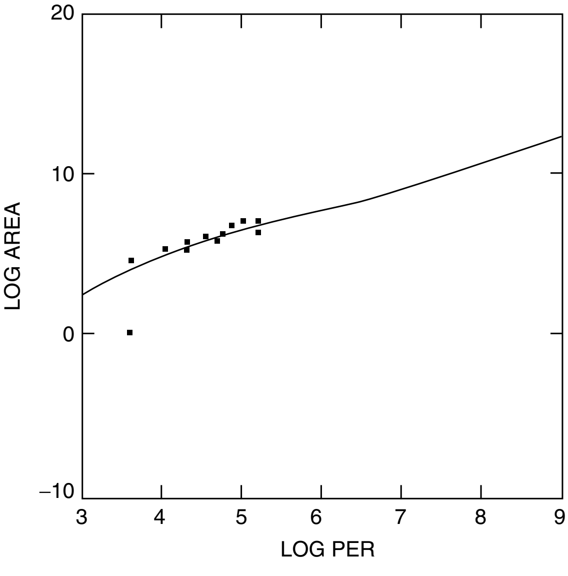


*Figure 8-9*. Plot of log area (natural logarithm of patch area) x log per (natural logarithm of patch perimeter). Smooth using Systat® DWLS method. Data from Fig. 8.8.

Table 8-7. *Quercus* woodland cover, analysis of Patch size and Perimeter (see Fig. 8.7 and Table. 8.2 for more details):

No Patch= code of individual patch
Area= Surface of patches
Perimeter= Length of patch edge
LogArea= Natural logarithm of patch size
LogPerimeter= Natural logarithm of patch edge
PiArea= Relative importance of each patch
PiPerimeter= Relative importance of each patch edge
piArea log(piArea)= to find Patch size diversity (Shannon diversity)
piPerimeter log(piPerimeter)= to find patch edge diversity (Shannon diversity)
H'a= Shannon diversity of patch size -∑piArea log(piArea)
H'p=Shannon diversity of patch edge -∑piPerimeter*log(piPerimeter)

| *No Patch Perimeter* | *Area* | *Perimeter* | *LogArea xlog (piArea)* | *Log xlog (piPeri-meter)* | *Pi Area* | *Piperi-meter* | *pi Area* | *piPeri-meter* |
|---|---|---|---|---|---|---|---|---|
| 1 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 2 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 3 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 4 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 5 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 6 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 7 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 8 | 100 | 37.660 | 4.605 | 3.629 | 0.001 | 0.005 | –0.008 | –0.026 |
| 9 | 200 | 57.660 | 5.298 | 4.055 | 0.003 | 0.007 | –0.015 | –0.036 |
| 10 | 200 | 57.660 | 5.298 | 4.055 | 0.003 | 0.007 | –0.015 | –0.036 |
| 11 | 200 | 57.660 | 5.298 | 4.055 | 0.003 | 0.007 | –0.015 | –0.036 |
| 12 | 200 | 75.310 | 5.298 | 4.322 | 0.003 | 0.010 | –0.015 | –0.045 |
| 13 | 290 | 110.970 | 5.670 | 4.709 | 0.004 | 0.014 | –0.021 | –0.061 |
| 14 | 300 | 76.490 | 5.704 | 4.337 | 0.004 | 0.010 | –0.021 | –0.045 |
| 15 | 300 | 112.970 | 5.704 | 4.727 | 0.004 | 0.015 | –0.021 | –0.062 |
| 16 | 400 | 96.490 | 5.991 | 4.569 | 0.005 | 0.012 | –0.027 | –0.054 |
| 17 | 500 | 117.660 | 6.215 | 4.768 | 0.006 | 0.015 | –0.032 | –0.063 |
| 18 | 500 | 188.280 | 6.215 | 5.238 | 0.006 | 0.024 | –0.032 | –0.090 |
| 19 | 500 | 116.490 | 6.215 | 4.758 | 0.006 | 0.015 | –0.032 | –0.063 |
| 20 | 780 | 189.800 | 6.659 | 5.246 | 0.010 | 0.024 | –0.046 | –0.091 |
| 21 | 800 | 134.140 | 6.685 | 4.899 | 0.010 | 0.017 | –0.046 | –0.070 |
| 22 | 1000 | 210.630 | 6.908 | 5.350 | 0.013 | 0.027 | –0.055 | –0.098 |
| 23 | 1100 | 154.140 | 7.003 | 5.038 | 0.014 | 0.020 | –0.059 | –0.078 |
| 24 | 1141 | 187.800 | 7.040 | 5.235 | 0.014 | 0.024 | –0.061 | –0.090 |
| 25 | 1300 | 304.770 | 7.170 | 5.720 | 0.016 | 0.039 | –0.068 | –0.127 |
| 26 | 4350 | 706.710 | 8.378 | 6.561 | 0.055 | 0.091 | –0.160 | –0.218 |
| 27 | 14591 | 1443.710 | 9.588 | 7.275 | 0.185 | 0.186 | –0.312 | –0.313 |
| 28 | 49602 | 3071.670 | 10.812 | 8.030 | 0.627 | 0.395 | –0.292 | –0.367 |
| Total | 79054 | 7772 | | | 1 | 1 | H'a 1.41 | H'p 2.25 |

Table 8-8. Minimum (min), Maximum (max.) and Mean of Patch size Area and Patch Edge (Perimeter) of oak woodland cover (see Tab. 8.7 and Fig.8.8 and Tab. 8.2 for more details).

| | *Patch size (Area)* | *Patch Edge Perimeter* |
|---|---|---|
| min | 100 | 37.660 |
| max | 4962 | 3071.67 |
| mean | 2823 | 277 |

The fragmentation that represents one of the major human induced disturbance effects can change the heterogeneity of a landscape, producing the effect of species distribution. Lacunarity seems a reasonable method to measure this heterogeneity (see also Dale 2000).

Cantor dust is a fractal object obtained by applying a generator to a unit interval that divides into three parts of equal intervals. The middle part is deleted. The two parts are then again divided, each into three parts. In five generations, the length of the segments is so short that it is not possible to distinguish the sixth generation. The fractal dimension of the triadic Cantor set is a fractal set with a fractal dimension $D=\ln2/\ln3$.

To calculate lacunarity, we utilize the "gliding box" algorithm according to Allain & Cloitre (1991), see also Plotnick et al. 1993.

A r × r box is moved from the upper left corner to the right lower corner by one step of one cell for each column and the number of occupied sites, according to the classes of box mass (Number of occupied sites).

$$\Lambda(r)=Z^{(2)}/(Z(1))^2 \quad (24)$$

$$Z^{(1)}=\Sigma SQ(S,r) \quad (25)$$

$$Z^{(2)}=\Sigma S^2Q(S,r) \quad (26)$$

The probability distribution is: $Q(S,r)=n(S,r)/N(r)$
$n(S,r)$ is the number of boxes in which a box mass category has been found.
The frequency distribution is : $N(r)=(M-r+1)^2$
$M=$ size of the map
The number of boxes of size r containing S occupied sites is indicated $N(r)$.

Lacunarity index is better understood considering this index as ratio of $\Lambda(r)=Z^{(2)}/(Z^{(1)})^2$ where $Z^{(1)}=S(r)$ the mean box mass and $Z(2)=ss2(r) + S2(r)$, $S(r)$ is the mean and $ss2(r)$ the variance of the number of sites per box. Then

$$\Lambda(r)=ss2(r)/S2(r) +1 \quad (27)$$

1. Lacunarity is a function of the gliding box. Larger box sizes have a lower lacunarity because in increasing the size of the box, the relative variance decreases.

2. Lacunarity is a function of occupied sites. The lower the fraction of P of occupied sites, the higher the lacunarity $ss2(r)/S2(r)$ and it goes to infinity

3. Lacunarity changes according the spatial arrangement of occupied sites. Large patches have higher lacunarity values then small patches.

The lacunarity analysis may be made using different maps with the same r, or different gliding box sizes for the same map.

Simulations conducted by Plotnick et al. (1993) on simulated maps with r ranging from 1 to 128 have demonstrated that the highest value of lacunarity is observed when r=1 and the grain size of the maps equal to the box size.

Lacunarity can be used also to analyze transect data.

### *8.2.2.4 Semivariance*

Semivariograms are utilized to measure variance at many scales, comparing the values of a random variable at two points at a given lag distance. Semivariograms are mostly used in geostatistics (Isaaks & Srivastava 1989).

$$g(g)=1/2N(g)\ \Sigma(Xj\text{-}Xj+g)2 \tag{28}$$

where g(g) is the semivariance at lag g, N(g) is the number of pair-wise comparisons at lag g and Xj is the random variate at position j.

The plot of semivariance g against the g lag allows one to see at what distance the variance changes.

The semivariance generally increases with increasing distance, although this is not true for all processes and is inversely related to the spatial autocorrelation of a variable.

From the two pictures in Figure 8.10 it is possible to assess that at a distance of about 150 km, there is the maximum of differences in density and that this decreases when we move to a biogeographical scale. Data from BBS do not have a asymptotic maximum semivariance and the maximum is reached at intermediate distance. This can mean that a species is more abundant around the central point of biogeographic distribution and that apart from this point, the abundance decreases, showing a higher spatial auto-correlation (Villard & Maurer 1996).

### *8.2.2.5 Measuring boundaries in the landscape*

This chapter considers ecotones as important structures in a landscape. These structures are inherent properties in a landscape but also function as shaping factors in many processes.

The detection of boundaries in a landscape is not a simple matter. In fact, the edges between two different habitats or land cover never have the functions of true boundaries. On the other hand, especially in human-dominated landscape boundaries they are so thin and the habitat constraint is so high that it is difficult to find a correlation between boundary structure and function.

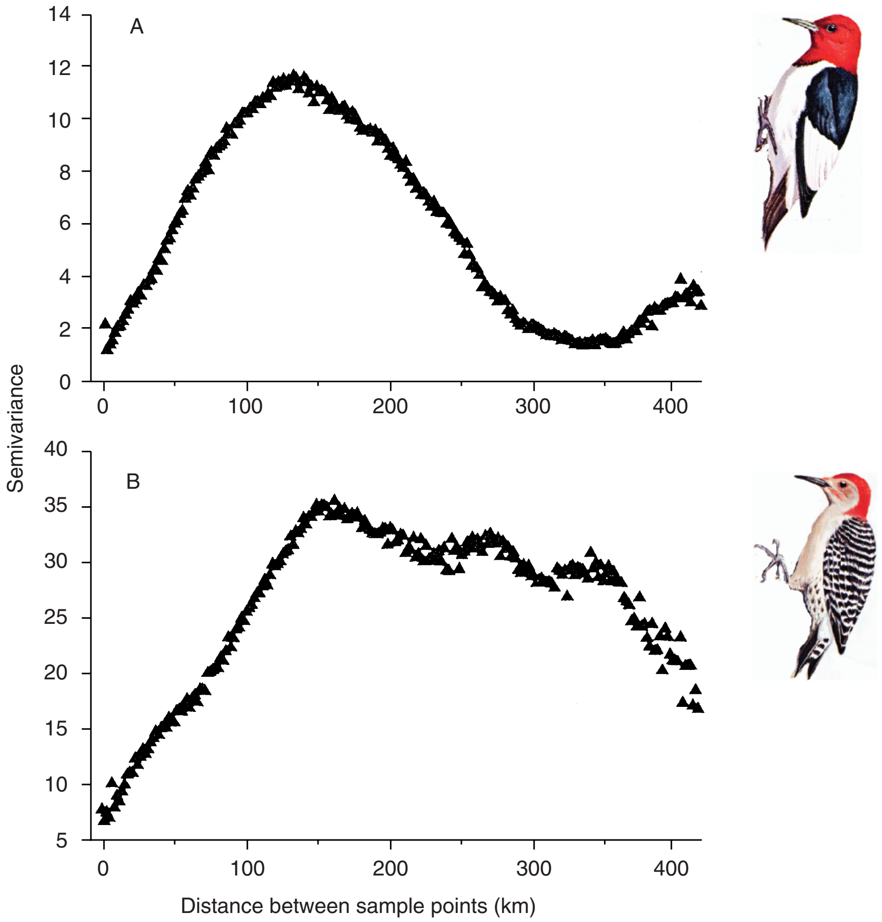


*Figure 8-10*. The semivariance has been calculated for two species of birds red-headed woodpecker *(Melanerpes erythrocephalus)* and red-bellied woodpecker *(Melanerpes carolinus)* (modified from Villard & Maurer 1996, with permission).

It appears clearer when studying the behavior of animals that often a boundary is perceived in the neighborhood of a physical edge. Therefore, the distance from this environmental discontinuity can be really important in the life history of a species.

The complexity of a landscape can be measured in terms of patch diversity and also in terms of boundary complexity and connectivity (Young & Jarvis 2001).

Due to the importance attached to boundaries in the dynamics and functioning of landscape, their measurement is a fundamental step to achieving a deeper knowledge of the structure and functioning of the land mosaic.

Recently, Metzger & Muller (1996) have elaborated a method to measure some relevant characters of a landscape assessed by remote sensing technology and presenting several indices of boundary proportion, landcover boundary complexity and landscape boundary complexity.

In section 8.5.3, more details are provided on the methodology.

### *8.2.2.6 Measuring fragmentation*

In order to measure the fragmentation of a region, several indicators are available, like the number of undissected areas, the average area and the density of the roads. Bowen's landscape dissection index LDI (Bowen & Burgess 1981) is described.

*Landscape Dissection Index*

$$LDI = \frac{\sum_{i=1}^{n} Pi}{\sqrt[2]{\pi At \sum_{i=1}^{n} Ai}} \tag{29}$$

where Pi = perimeters of the n patches, Ai = size of patches, At = total size of the landscape.

## 8.3 THE FRACTAL GEOMETRY APPROACH

### 8.3.1 Introduction

Heterogeneity is a common pattern in the environment and is visible, especially at the landscape scale. Organisms, populations and communities have a spatial distribution that reflects the heterogeneous nature of the land.

The unequal distribution of natural phenomena such as the geological nature of rocks, the rain distribution across a mountainous range or the distribution of tree cover in a watershed, all create complicated mosaics to which organisms react.

To measure this complexity, Euclidean geometry often seems inadequate and new approaches are required, in this, fractal geometry seems to fit the bill (Mandelbrot 1983; Feder 1988; Milne 1991; Hastings & Sugihara 1993).

In man-made landscapes in which straight lines and regular geometric figures have been created, transforming wild land into rural or urbanized areas, Euclidean geometry may be utilized to describe simple spatial patterns such as perimeter/area ratio, patch area and patch distance. When we consider a more natural landscape, such figures disappear and the irregularity of the patches reduces most of the descriptive capacities of Euclidean geometry.

Fractal geometry brings a new perspective to studying and interpreting landscape complexity and dynamics across scales. The aim of this section is to introduce to the use of fractal geometry in landscape research, producing a simplified view of a very complicated mathematical approach and reporting examples from a large variety of scales, from landscapes to individuals.

Fractal geometry is useful in landscape analysis because the hierarchical complexity of the landscapes and their scaled patterns and processes need powerful tools to be investigated. Fractals are represented not only by patterns such as forest patch shape, but also by processes and this last component appears extremely useful.

Fractal analysis can be applied not only to patch shape and spatial arrangement but also to the distribution of animals in the space.

### 8.3.2 Concepts and definitions

The word fractal was coined in 1975 by Mandelbrot to describe an irregular object in which the irregularity is present at all scales, scale-invariant. Mandelbrot (1986) proposed this definition "A fractal is by definition a set for which the Hausdorff Besicovitch dimension strictly exceeds the topological dimension." A fractal is a shape made of parts similar to the whole in some way. Fractals can be considered objects or patterns that have non-integer dimensions.

When a fractal object has qualities of the patterns at coarse scale, which are repeated at finer and finer scale, this object shows self-similarity (Figure 8.11).

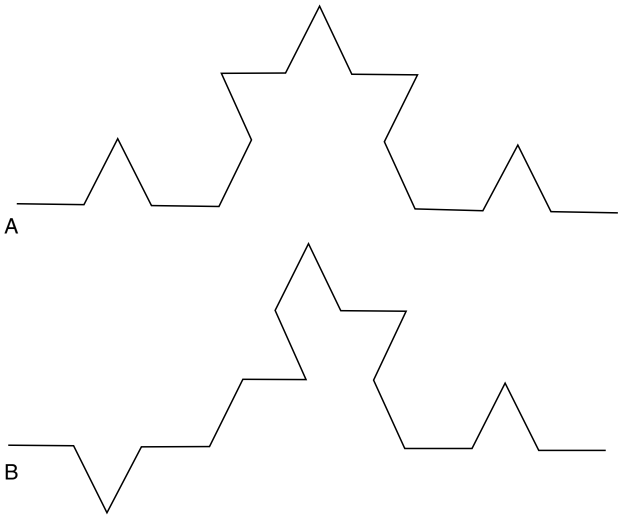


*Figure 8-11*. Example of regular (A) and a randomized (B) Koch snowflake.

Two different types of fractals can be distinguished: regular fractals and random fractals. The first type is represented by scale invariant (self-similarity or self-affine) objects (Figure 8.12). Regular fractals have exact self-similarity. When an object is a rescaled copy of itself in all directions (isotropic), it has a self-similarity attribute. When the rescaling is anisotropic, the object presents a self-affinity.

The second category pertains to natural fractals (clouds, coastlines, organism abundance in the space, etc.). Generally, most of the natural fractals deviate from linear self-similarity and are called random fractals and display a statistical version of self-similarity.

Related to self-similarity is the concept of scale-dependence. For instance, the coast is a fractal object for which the total length depends on the scale of resolution at which the measure is done. The complexity is measured with the fractal dimension D, which is the counterpart of the familiar Euclidean dimensions 0 (point), 1 (line and curves), 2 (surfaces), 3 (volumes) and it is never an integer. In a regular one-dimensional object, the mass increases in proportion to the length, say 2R. The mass in a two-dimensional disk with radius R increases in proportion to $\pi R^2$, the area of a circle, in a three-dimensional object the mass increases of 4/3 $\pi R^3$, which is the volume of a sphere. Adding dimensions, the mass increases according to the power of the number of dimensions. In fractal objects, the R is raised to some power Dm that is not an integer number.

The fractal approach is intuitively easy to understand but it is necessary to develop and apply this theory to practice. For further information on fractal geometry, we recommend Mandelbrot (1983), Hasting & Sugihara (1993), Feder (1988) and Frontier (1987).

Fractal geometry finds a broad range of applications in different disciplines of the natural sciences such as geology (Loehle & Li 1996; Acuna & Yortos 1995),

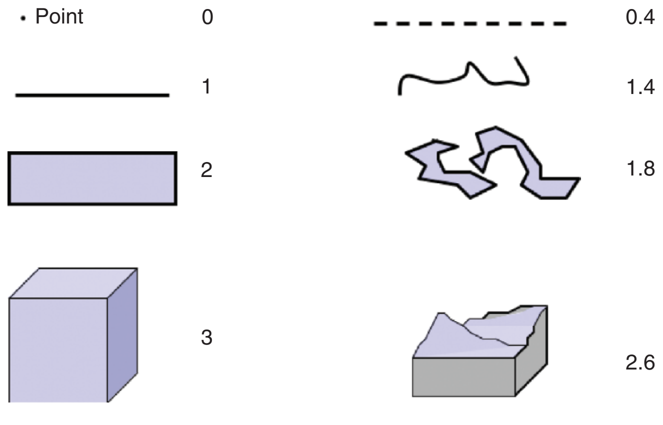


*Figure 8-12*. Comparison between Euclidean dimensions (left) and fractal dimensions (right).

hydraulics (Ichoku et al. 1996), soil composition (Perrier et al. 1995; Barak et al. (1996), dynamics ( Perfect & Kay 1995; Perfect et al. 1996, Rasiah 1995), microbial transport (Li et al. 1996), vegetation structure (Chen et al. 1994).

Fractal geometry is particularly useful in the study of phenomena that have ambiguity according to the scalar properties. The coastline length is a classic example. The length of the coast depends on the measuring unit. In this case, increasing the size of the unit from meters to kms, the total length of the coast decreases. Thus, the length of a coast is scale dependent and relating this measure to the size of an organism such as a sea otter or a crab, it is possible to adopt the right measurement scale at which an organism is sensitive. This consideration can be made for human-related phenomena and, for instance, the number of suitable harbors along the coasts decreases as the size of the ships increases.

Many patterns and processes are scale-dependent and fractal model can describe their characteristics without the ambiguity of Euclidean geometry.

For this reason, fractals seems more and more important in landscape ecology and related sciences.

The scale properties of the objects measured using fractal geometry require more clarification on the scale attributes. The components of scale are lag, window, spatial and/or temporal extension of observed quantities and the grain of the resolution (Turner et al. 1991). Other details presented in Chapter 3 are devoted to the scale concept.

Fractal models can be applied to measure landscape characters but also to measure patterns perceived to be species-specific (Johnson et al. 1992). Both approaches are extremely useful to understand the complexity of the environment and to predict species-specific replies to the spatial configuration of resources (Figure 8.13).

Examples of application to riparian forest patches are shown by Rex & Malanson (1990). Leduc et al. (1994) combined fractal analysis to variogram techniques to estimate the fractal dimension of a fragmented landscape.

van Hees (1994) measured the complexity of Alaskan vegetation, applying the fractal technique of the dividers method.

Lathrop & Peterson (1992) used the fractal approach in identifying structural self-similarity in a mountainous landscape by measuring the area-perimeter relationship.

In the next points, we will discuss examples of the application of fractal geometry to landscape structures and to animals moving and acting in the landscape.

### 8.3.3 The fractal dimension of the edges

Many processes and organisms are sensitive to patch shape but the measure of the patch convolution is difficult to accomplish using Euclidean

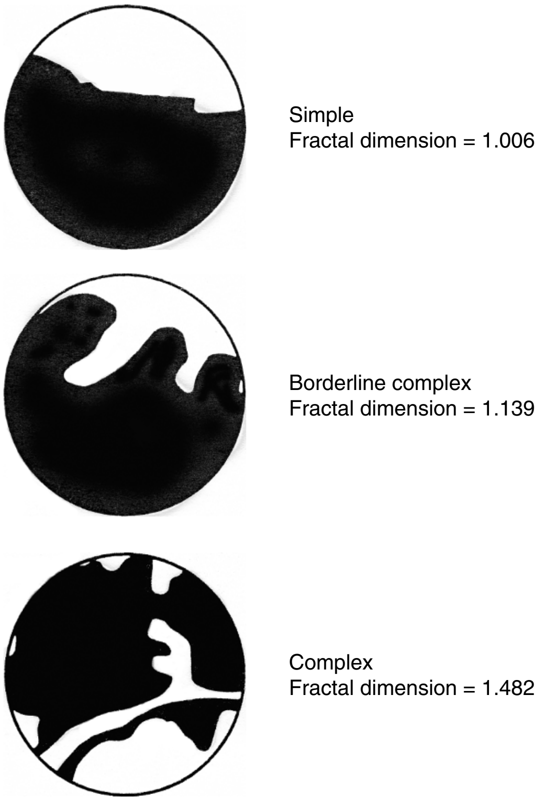


*Figure 8-13*. Example of different complexity of a vegetation border expressed by the fractal dimension D, note that the increase of edges is equivalent to the increase of fractal dimension (from Hees 1994, with permission).

geometry. The fractal approach to studying edge complexity takes into account the scale at which an edge is measured and the length of the ruler we use to measure it (Figure 8.13).

In other words, the length of objects like coastlines, rivers and mountain ridges depends on the measurement scale L. Assuming C(L) and the number of steps necessary to cover the total length $C(L)=kL^{-D}$, the total length will be

$$TOT(L)=C(L)xL$$

then

(1) $TOT(L)=kL^{-D}xL=kL^{1-D}$

According to a simple power law where TOT(L) is the length of the object (coastline, rivers, etc.) measured at scale L, D ($2>D<1$) is the fractal dimension and k is a constant. Increasing L reduces the total length TOT(L), and *vice versa* if L is smaller.

Transforming it into a logarithmic form equation (1) will become

$\log TOT(L)=\log k+(1-D)\log L$

Regressing $TOT(L)$ and $\log L$, $1-D$ will be the angular coefficient $m=1-D$

For Euclidean object $D=1$, the length is independent of the measurement scale.

For a fractal object like Koch's snowflake, the fractal dimension $D=1.26$.

This power law has been applied to study the tortuosity of the pathway of insect movements (Wiens et al. 1993). In fact, fractal dimension is a scale-independent measure of the tortuosity of a pathway (Wiens et al. (1995). D is calculated regressing ln (natural logarithm) of path length $C(L)$ and the ln of length scale L, which is subtracted from 1 to yield D.

K is the intercept of the regression line. When the pathway is a straight line $D=1$ and when the pathway is so complex as to fill a plane $D=2$. In general, we can assure than the more a pathway is tortuous (high value of D) and the more the organism interacts in fine grain with the heterogeneity of the landscape.

$C(L)$ may be measured approximately but easily by using the Grid method (Sugihara & May 1990), which consists in superimposing a regular grid of side length L on to the pathway or the edge of interest. At every L size, grid, the squares containing a piece of the pathway or edge are counted. Then the natural log (ln) of the total number of squares is regressed with the L. D is equal to slope of the regression minus 1. See figure 8.14 and 8.15.

## 8.3.4 The fractal dimension of patches

The complexity of a polygon is expressed by the relationship $P\approx\sqrt{A}^D$ (i.e. $\log P\approx 1/2_D \mathrm{Log}\, A$) where P is the perimeter and A the area. For simple polygons such as circles and rectangles $P\approx\sqrt{A}$ and $D=1$. For irregular and complex polygons the perimeter tends to fill the plane and $P\approx A$ with $D \longrightarrow 2$.

This relationship can be used to calculate the complexity of the coast lines of various islands, or the complexity of vegetation patches using the same scale of measurement and assuming a self-similarity between islands or vegetation patches of different size. In this case, the scale of the ruler should be small enough in order to avoid that with the decreasing island perimeter-area the measured shapes become Euclidean ($D \longrightarrow 1$).

The fractal dimension is obtained by regressing $\log(P)$ on $\log(A)$, where $D=2\mathrm{x}$regression slope. Bogaert (2000) (Figure 8.16) has found by approximation the fractal dimension

$$D=2\ln P/4/\ln A.$$

Using this approach, Krummel et al. (1987) have demonstrated that the fractal dimension changes according to the size of the forest patches. Moving to small woodlots, mainly produced by human disturbance to large forests, less –

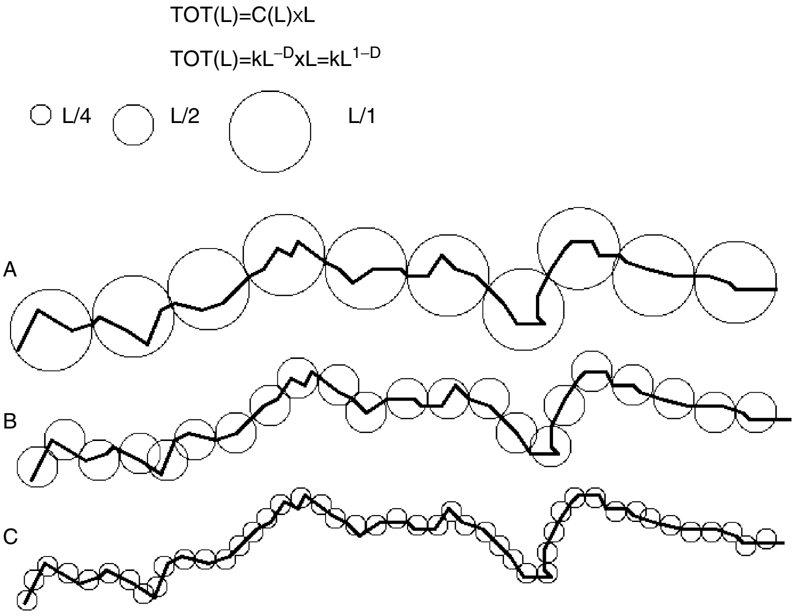


*Figure 8-14.* The irregularity of a border can be estimated by calculating the fractal dimensions applying the caliber method. In this case, the total length of the border decreases with the increase of the caliber size. In A the caliber is L/1, the number of steps C(L)=10, the total length TOT(L)=10x1=10; in B L/2, C(L)=22, TOT(L)=22x1/2=11, in C L/4, C(L)=47, TOT(L)=47x1/4=11.75. The shorter the caliber the more border will be measured, see text for the calculation of the fractal dimension (from Farina 2001, with permission).

disturbed, the fractal dimension shows an increase. This means that at a larger scale, where the natural processes are dominant, the landscape is more convoluted. On the contrary, at a small scale, the patterns are more regular and simplified and most of these patterns have been produced by human disturbance regimes. In terms of fractal analysis, this means that moving across the scale, the invariance is respected in two distinct sub-sets. A first set is dominated by human disturbance regimes, a second step is dominated by natural processes (Figure 8.17).

This approach is very interesting and can be applied to a broad range of phenomena in which shape is an important component of the ecological process.

## The Box Grid Dimension

Patch shape can be measured, assuming that the patches and the number of necessary boxes to cover the object are in a power law relationship.

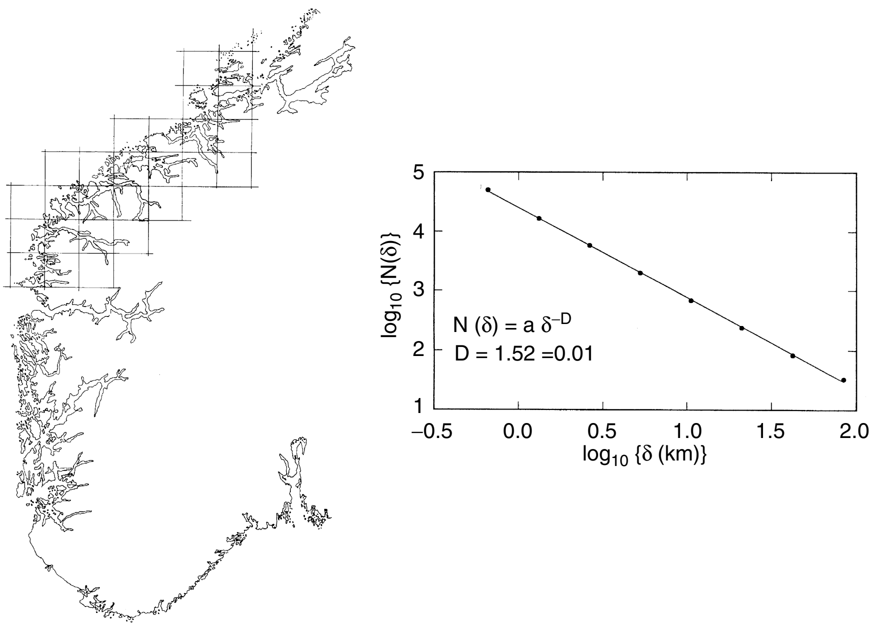


*Figure 8-15*. Example of application of fractal geometry to the computation of the complexity of an edge. The coast of southern Norway with a superimposed square grid of $\delta\tilde{}$ 50 Km and the log-log plot of $N(\delta) = a\delta^{-D}$. Changing the value of $\delta$, and regressing the number of boxes $N(\delta)$ of d dimension that cover the coast line with the value of $\delta$, the fractal dimension D is the (-1) times the slope of the regression. This method is applied in Box 6.7 (from Feder 1988, with permission).

Assuming L to be the length of the box, the number of boxes necessary to cover the patch will be N(L), the number of boxes are related to their dimensions by the equation

$$N(L)=kL^{-D}$$

The exponent is negative because the number of boxes decreases with the increase of the box length L. Transforming the equation in the logarithmic form

$\text{Log } N(L)=\log k - D\log L$
D is calculated regressing L with N(L).

It is possible to use the length of the box instead of using the area of the box A(L).
$A(L)=N(L)xL^2$
$A(L)=kL^{-D}xL^2$
$A(L)=kL^{2-D}$

The fractal dimension is calculated by regressing the area of the box that covers the patch investigated with the length of the box D=2–m, where m is the slope of the regression line.

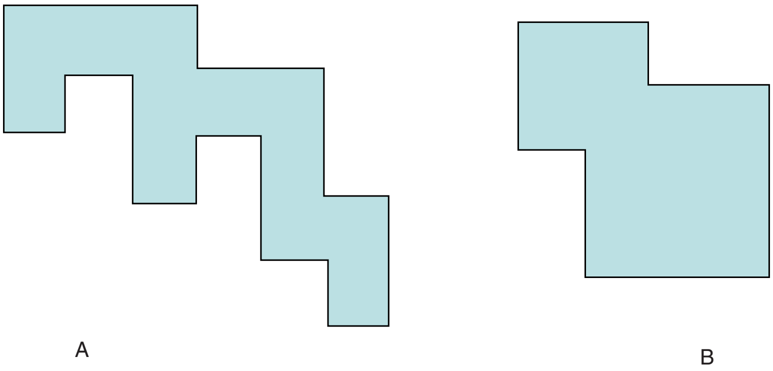


*Figure 8-16*. Two patches with identical surface areas (Aa=Ab =12) but with a different perimeter (Pa=26, Pb=16) have respectively a fractal dimension of A=1.50, B=1.11 (the dimension has been calculated according to Bogaert 2000, see text (from Farina 2001, with permission).

*The Cluster (mass) dimension*

This method consists in the study of a favorable cover around a focal cell. Here, a sliding window is passed through the matrix of variable sizes according to the process or the organismic function that we intend to test.

Considering that the size of favorable habitat O(L) increases with the increase of the sampling window as a power law $O(L)=kL^D$, where D is the

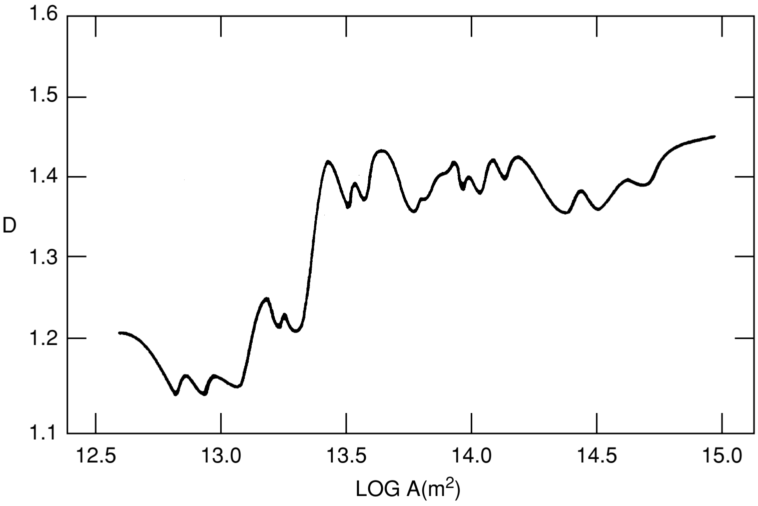


*Figure 8-17*. The fractal dimensions change abruptly when a change of the scale of resolution reflects the change between human shaping of the landscape mosaic (small scale) to natural shaping forces (largest scale). D = fractal dimension, Log A = logarithm of area investigated. (from Krummel et al. 1987 with permission).

amount of habitat expected for a window of size L. D can be calculated as the angular coefficient of the regression $\log O(L)=\log k+D\log L$.

### 8.3.5 Semivariance and fractal analysis

Russel et al. (1992) have studied sea bird dispersion and the distribution of food by applying fractal analysis In this study, to assess the relationship between prey and predators, the authors have utilized a method based on geostatistics and regionalized variables (RV) theory. This regionalized variable is too complicated to be expressed by a simple mathematical model because it has the deterministic character of the nearby samples, but is stocastic in the sense that value at a given point because cannot be calculated from neighboring samples.

The semivariance $g(\gamma)=1/2N(\gamma)\ \Sigma(Xj-Xj+\gamma)^{2})$ is in relation with $\gamma$ (that is the sampling interval) by the relationship: $2g(\gamma)=\gamma^{(4-2D)}$ where $g(\gamma)$ is the semivariance at g interval, the fractal dimension

$$D=(4-m)/2\ (\gamma \to 0)$$

where m is the slope (4-2D) of $\ln g(\gamma)-\ln \gamma$ (Burrough 1981).

Fractal analysis is particularly efficient to describe variation across a wide range of scales. Generally, the patterns are produced by a variety of processes operating at many spatial scales and levels of organization.

Fractals help our understanding of ecological processes operating although *per se* the information cannot be correlated with a specific process.

Fractal analysis has also been used for computing the home ranges of animals (Loehle 1990), employing box-counting using boxes of different sizes to assess the pattern of a occupation of a space by an object. In the case presented by Loehle, a radio-collared hawk visited the “home range” in an irregular manner: some areas were more frequented but others were never visited. If we encircle the whole area as the maximum distance in which the animal has been observed, we lose many details. On the contrary, considering the birds movements at a different spatial scale, we can measure the complexity in the area covered from the roosting place to the entire landscape.

### 8.3.6 Examples of the application of fractals to animal behavior

If we adopt the organism-centered view of the landscape it is essential to know the perception resolution or grain and the range of scale, the extension at which an organism considers the landscape to be heterogeneous.

Grain and extension can change during the development of the organism (e.g., fish size classes) and can change according the seasons (e.g., migratory birds). This can create problems of employing too simple or too sophisticated models.

The movements of animals are easily detected and measurable for many species. These movements are strongly affected by the body mass of the organism and by the resolution at which the organism perceives the surroundings (Figure 8.18).

Considering that a landscape is a hierarchical array of patches, it is important to distinguish at what resolution the organism perceives its surroundings. In such a way, the organism ignores the patterns outside its specific range of resolution.

If we use the movement of the organism as an indicator of landscape interaction, we can assume that species which move slowly perceive the environment at a finer scale than species moving faster. But when two species have different sizes it seems impossible to compare their behavior and resource use because they are scaled differently.

In fact, movement pathway is strongly influenced by landscape structure and the size of the organism. The body size-scale dependent movements are difficult to compare.

Applying a fractal analysis, it is possible to afford a scale-independent measure of the movements because the fractal dimension of a movement

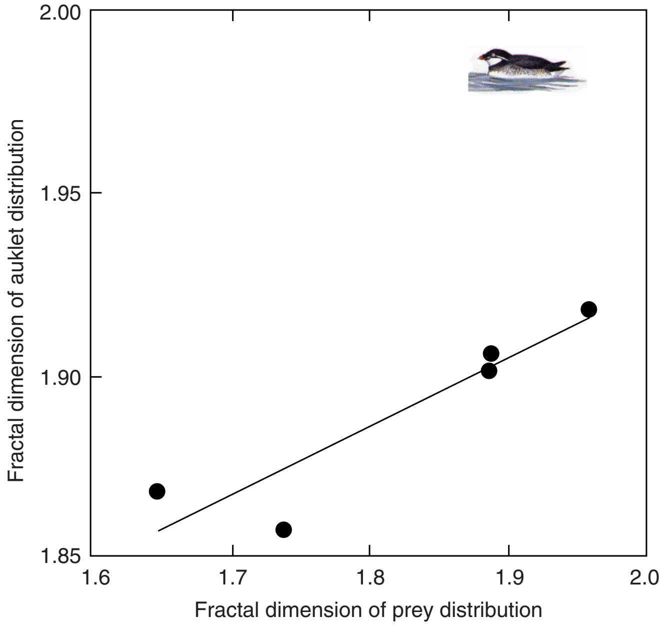


*Figure 8-18*. Significant relationship between the fractal dimension of the lesser auklet (*Aethia pusilla*) distribution and prey, across six transects (from Russel et al. 1992, with permission).

pathway is scale-independent and may be used to compare different taxa (Wiens et al. 1995).

A clear example of such an approach is presented by With (1994), studying the movement patterns of three acridid grasshoppers (*Orthoptera*) in a grassland mosaic. Manipulation of species in a controlled microlandscape had been carried out by the author, confirming the predictive potentiality of such an approach to broad-scale experimentally intractable landscapes.

The larger species *Xanthippus corallipes* moved at a faster rate than the two other species *Psoloessa delicatula* and *Opeia obscura* and a perceived the microlandscape in a different way, presenting different values of fractal dimension D. This species has more linear movements than the two others that perceive the heterogeneity of the landscape to a lesser degree. These two species have a similar D value and this probably means they use resources in a similar way (Figure 8.19).

To calculate the fractal dimension (D) the divider method was employed. It consists in measuring the total length of the pathway (summation of distances between the points) at different "ruler" lengths. In this case, 25 ruler lengths were selected. The minimum ruler length was calculated as the average distance between the points and the maximum as 1/3 of the total path length, considering that at least three points are required for a linear regression.

For instance, Wiens et al. (1993) have found in three tenebrionid beetles living in prairie in northeastern Colorado, a similar D dimension of pathway convolution differing significantly from 1 (linear movement) and from random walking but these three species, although different in size and speed, have similar D dimensions demonstrating a similar strategy across the scale.

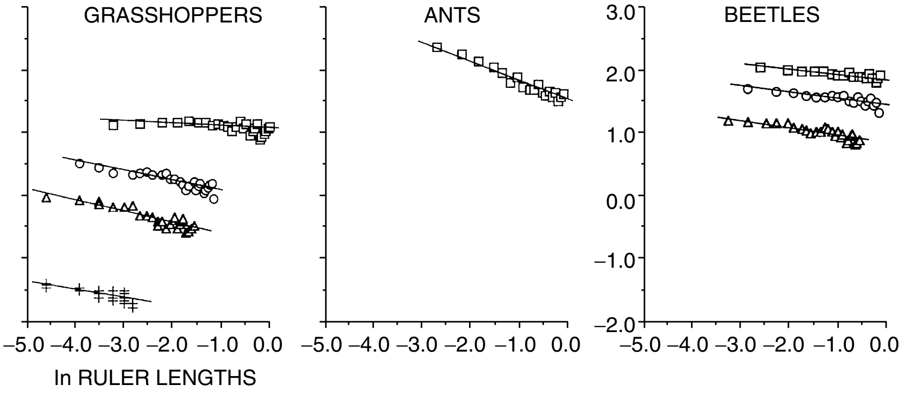


*Figure 8-19*. Regression showing the relationship between the pathway length (Y axis) and the measurement scale (X axis) in grasshoppers, ants and beetles. Grasshoppers: A=*Opeia obscura* nymph, B=*Opeia obscura* adult, C=*Psoloessa delicatula*, D=*Xanthippus corallipes*; Ants: E=*Pogonomyrmex occidentalis*; Beetles: F=*Eleodes extricata*, G=*Eleodes obsoleta*, H=*Eleodes hispilabris* (from Wiens et al. 1995, with permission).

Fractal analysis has been applied to study stress in the *Capra pyrenaica* caused by pregnancy and by *Sarcoptes scabies* infection (Alados et al. 1996). Owing to the increase in metabolic rate due to the infection stress, the infected animals show a reduction in the complexity of exploratory behavior. It is well known that the complexity of biological tissues decreases under the effects of pathologies. In the same manner, the behavior suffers a reduction in variability. Head-lift behavior, which consists in the interruption of feeding behavior and in lifting the head as antipredatory vigilance, was analyzed to be regressing. After a log-log linearization, the frequency of head-lifts where F(Δt) is the frequency of head-lifts at the time intervals of duration $\Delta t F(\Delta t)=k(\Delta t)^{D}=k(1/\Delta t)^{-D}$, where k is constant and D is the fractal dimension.

In Figure 8.20, the log-log regression of F(Δt) x Δt shows a reduction of the fractal dimension between non parasitized females (a) and parasitized female (b).

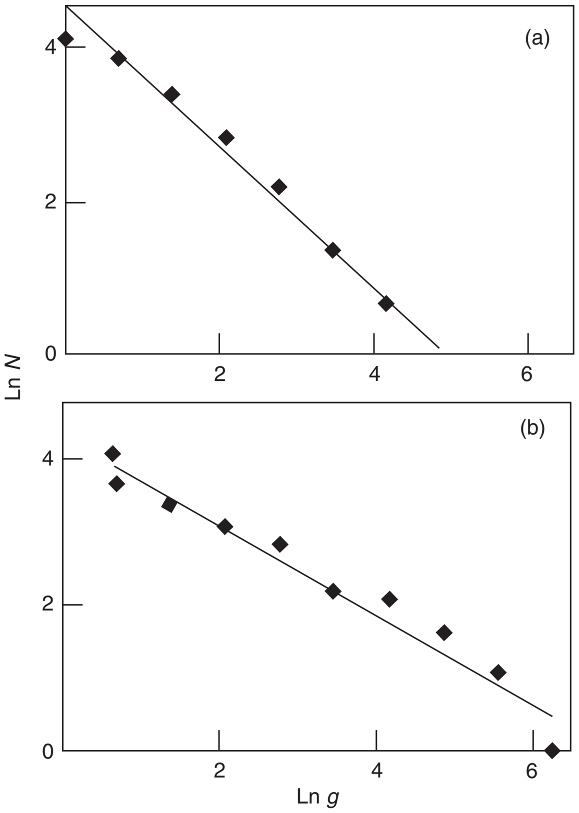


*Figure 8-20*. Log-log plot of the cumulative frequency (N) of feeding gaps greater or equal to a g interval in *Capra pyrenaica* (a) in parasitized, (b) in non-parasitized females (modified from Alados et al. 1996, with permission).

The feeding gap frequency N with frequency G greater or equal to a determined size g fits a power law N(g≥G)=kg-B where k is constant g= 1, 2, ...2ns and B is the korcak-Mandelbrot exponent.

## 8.4 GEOGRAPHIC INFORMATION SYSTEMS

### 8.4.1 Introduction

Geographic information systems (GIS) are a technology for handling spatial data. Developed in recent years, it is now applied in many fields from the local to the global scale. GIS is a configuration of computer hardware and software to capture, store and process spatial information, both numerical and qualitative, creating and updating maps, a technology for combining and interpreting maps, a revolution in map structure, content and use. The GIS can be classified in an alternative way and according to the application, addressed as Urban Information System, Spatial Decision Support System, Soil Information System, Planning Information System, Land Information System, etc.

The spatial information represented by the localization in a geographic space of attributes of an event can today be, easily handled and processed thanks to the combination of spatial statistic, mathematical procedures and computer hardware.

The combination of these three components creates a Geographic Information System or GIS (Burrough 1986), in which computer cartography, database management, remote sensing procedures and computer-aided design represent the structuring components (Figure 8.21).

GIS are used by a growing number of people in different fields from geography to economy, to social science and planning. There are GIS for many purposes; some are devoted to cartography, others to handle cartography and databases, others to process remote sensing information.

The GIS procedure may find a great number of applications in many fields such as geography, economy, social sciences, cartography, urban planning, etc. The dimension, software and technical requirements (hardware) range from a few Kb to many Gb, with costs from a few dollars to several thousand. Some are extremely user friendly; others need a dedicated operator (Figure 8.22).

The incredible development of these systems create difficulties in describing the several applications available, rooted in geography, computing and application areas (Walsh et al. 2003).

In landscape ecology, GIS is a fundamental tool, especially if it is used as a platform to manipulate models and real data, transferring information from implicit to explicit analysis.

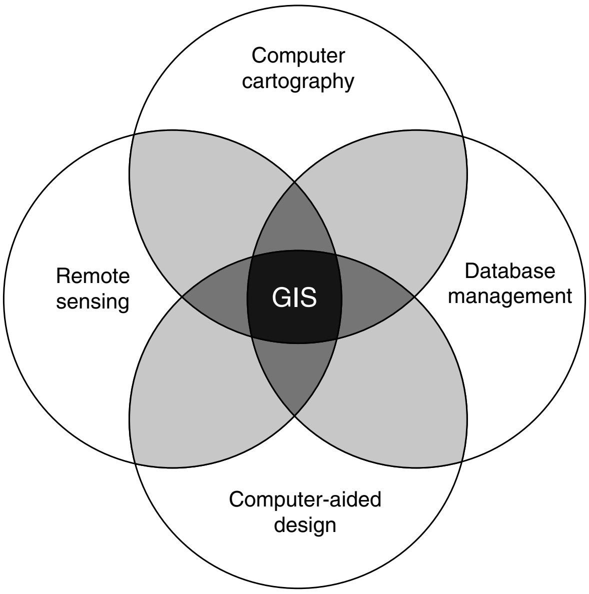


*Figure 8-21*. GIS is the combination of different procedures and methodologies (from Maguire 1991, with permission).

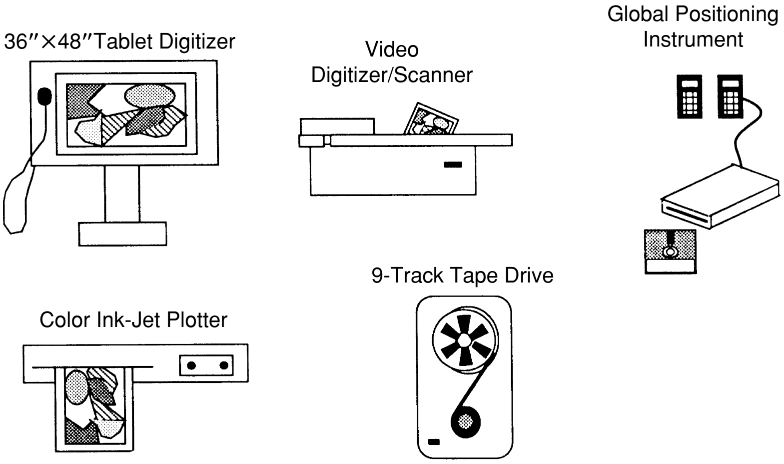


*Figure 8-22*. Components of a GIS laboratory. The complexity and the costs of the hardware and of the driving software are extremely variable. Often it is necessary to have large central computer memory to harvest digital images. Different softwares are necessary for coupling with the GIS software, especially to manipulate remote sensing data (from Coulson et al. 1991, with permission).

The GIS appears indispensable for most landscape investigations like:

Land use change
Vegetation patterning
Animal distribution across the landscape
Linking remote sensing with topography
Modeling processes across the landscape

## 8.4.2 The information process

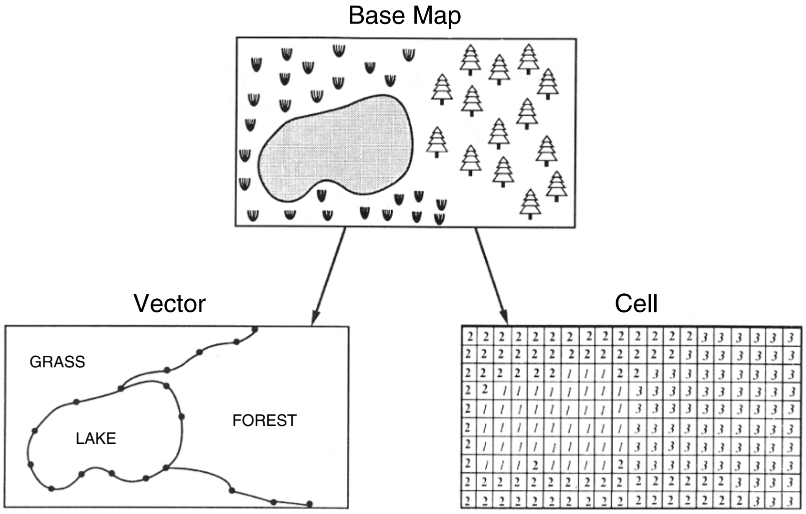
Three types of information on landscape features considered by a GIS are:

Name and characteristic of the features
Their locations
Their spatial relationship to one another

## 8.4.3 The representation of the spatial information

Two systems are available to represent the spatial information as lake-forest-field maps: raster and vectorial (Figures 8.23 and 8.24).

The raster format is the representation of a feature by using discrete units "pixel" or cells. The vectorial format utilizes the position of point, line and area and their connectivity. Advantages and disadvantages of both systems are summarized in Table 8.8.



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| 2 | 1 | 1 | 1 | 2 | 1 | 1 | 1 | 1 | 2 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 | 3 |
| 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 | 3 |
| 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 2 | 3 | 3 | 3 |

*Figure 8-23*. Representation of raster and vectorial format of a map (from Coulson et al. 1991, with permission).

## 8.4.4 GIS organization

Data in a GIS are represented by a hierarchy of information that have at the highest level

Cartographic models
Map layers
Titles
Resolutions
Orientations
Zones
Labels
Values
Location
Coordinates

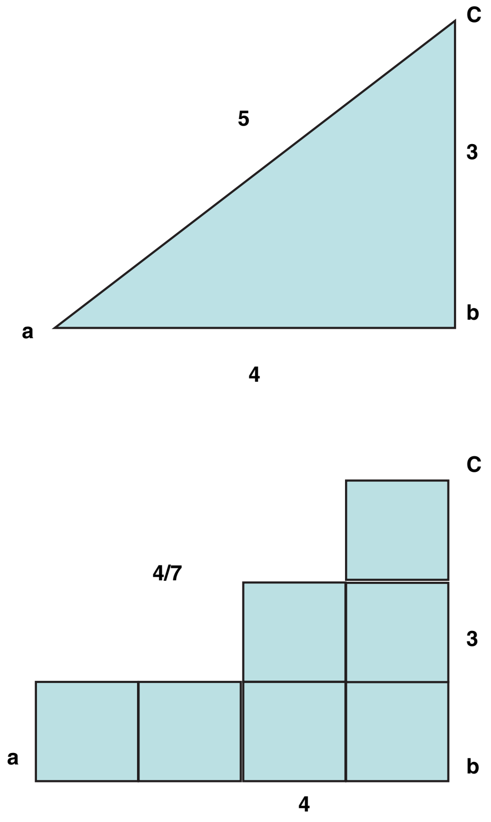


*Figure 8-24*. Raster versus vectorial representation of the reality. The real measures in raster format are coded and some biases in estimation have to be considered (Burrough 1986, with permission).

A GIS operates in geographical or virtual space in which every element (both in raster as in vectorial format) is indicated by a couple of coordinates (X,Y) and, consequently, every computational procedure is available either inside a layer or map or between different layers (Figure 8.25).

### 8.4.5 Cartographic model

The cartographic model is the collection of the map layers and describes a well-defined area. The map layers contain information on the same geographic area such as size, name of localities, history of special sites, etc. Each cartographic model has an implicit and explicit form.

### 8.4.6 Map layer

Often indicated simply as a layer, it is a conventional map reporting a variety of information, not necessarily geographical. In a map layer, information is represented by occupied cells described according to different attributes of the subject.

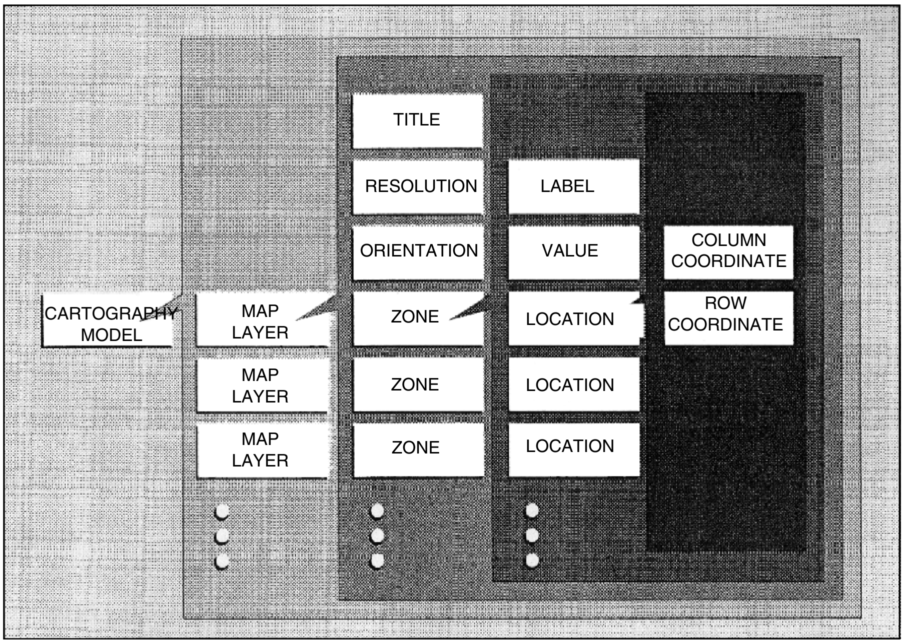


*Figure 8-25*. Scheme of the hierarchical organization of geographic data (from Tomlin 1990, with permission).

A layer contains other explanatory information such as: title, resolution, orientation and zone(s).

Titles such as "vegetation", "bird richness" are important when layers are manipulated and each layer enters in an algebric formula.

Resolution of a layer represents the relationship between ground and "on paper" distance.

Orientation of a layer indicates the relationship between geographic and cartographic direction.

Zones is a part of the map distinct for some attributes from other zones. For example, a forest patch, a field, urban area, etc. Each zone is indicated by a label that is a name, the values that form a further specification of the zone. For example, a zone labeled "forest" with a value of 200 "forest 200 m from road". Value can be expressed as ratio, interval, ordinal and nominal. Nominal is the representation of a quality of a zone, as "dense shrubland".

Location is the elementary unit of a map. In raster format it is represented by a square cell or grid cell, and by pixels or picture elements in image processing.

Coordinates are a pair of numbers expressed in geographic units, for example the distance in meters from the Equator and Greenwich, or simply by an "on-paper" numerical scale.

### 8.4.7 Procedures for cartographic handling and modeling

Most of the GIS available today have in common the capacity to manipulate the information at a single location and at the scale of the entire map.

Data are the recorded facts that in landscape ecology may be vegetation cover, land use, etc. All data in a GIS occupies a precise position located according to true geographical or working coordinates (x,y). In the first case, it may be UTM (kilometric coordinates).

### 8.4.8 Capturing data

Data are be captured in many ways, it is less expensive to rasterize existing maps such as topographic maps, land cover maps, etc.

Data can be already in raster format if provided by remote-sensing satellite stations.

Digitalization is a very precise but expensive procedure.

For example, the location with coordinates xij yij in which i is the attribute (land cover type) and j is the layer, can be manipulated algebraically by adding the same location in other layers xij yij + xim yim (where m is another layer.)

Other procedures can manipulate entire layers *this map* + *that map* = *new map*

## 8.4.9 Some cartographic modeling procedures

According to Tomlin (1990), at least four operations are available in GIS procedures:

Local operations: for each location it is possible to associate a new value that represents the transformation of the same value by applying mathematical functions to each location's value(s) on one or more existing map layers.

Zonal operations: for each location it computes a new value as a function of the existing value from a specified layer.

Focal operations: for each location it computes a new value according to the character of the neighboring locations of the same map layer or on other map layers (Figure 8.26).

## 8.4.10 Commands in GIS

Many routines are available to transform data.

For local operations arithmetic, menus are available (Larsen & Hulse 1989) that have functions such as:

*add* : adds values of two or more existing maps
*average*: averages values of two or more existing maps
*cover*: covers values of one existing map with one or more existing maps
*divide*: divides values of one existing map by one or more existing maps
*maximize*: maximizes values of two or more existing maps on new maps
*minimize*: minimizes values of two or more existing maps on a new map

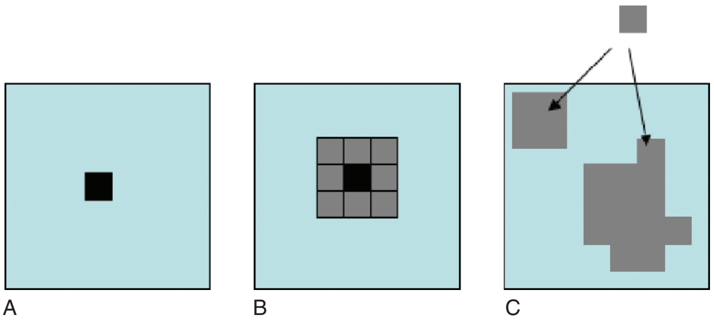


*Figure 8-26*. The fundamental capabilities of a GIS can be summarized in three groups of procedures: (a) functions of a single value, (b) functions within neighborhoods, (c) functions of entire zones (from Tomlin 1990, with permission).

*multiply*: multiplies values of two or more existing maps

*subtract*: subtracts values of one existing map from one or more existing maps.

For focal operations, a neighborhood menu is available with functions like:

*clump*: generates a map of contiguous like-valued cells
*differentiate*: generates a slope map from surface data
*interpolate*: calculates intermediate values from two positions
*orient*: generates an aspect map from surface data
*radiate*: generates a viewshed map from specified viewer locations
*scan*: classifies neighborhood of specified locations as to neighboring values
*score*: compares and summarizes values of two maps on a point-by-point basis
*smooth*: generates map of surface from map of contours
*spread*: generates map of proximity to specified locations

### 8.4.11 GIS and remote sensing

Remote-sensing information produced by satellite or aerial photo have to be interpreted before being used in a GIS. Generally, data from Remote Sensing are imported in a GIS after classification and georeferentiation.

The procedures of land classification are independent of GIS techniques but when the data have to be introduced into a GIS, it is necessary to know at least the spatial scale (the resolution) of the images for georeferentiation.

### 8.4.12 Scaling in GIS

In landscape ecology it is often useful to process spatial data at different scales; in fact, in a landscape, patterns and processes are visible and function along a broad range of spatial scales (Turner et al. 1989). Actually, a limited number of routines are available to carry out these procedures. Baker & Cai (1992) has presented a program operating in GRASS, able to calculate more than 60 routines on landscape structure (e.g., distance, size, shape, fractal dimension, perimeters, diversity, texture, juxtaposition, edges), with different possibilities of sampling areas of several sizes, changing 15 scales of analysis or using a moving window.

### 8.4.13 Key study n. 1

Ecotope classification, application of cartographic modeling to the Aulella watershed (Farina 1996).

The classification of a landscape into the component ecotopes is a common procedure in landscape analysis. The ecotope represents a piece of land in which some characters are homogeneous and distinct from neighboring areas. The characters are often the combination of physical and biotic components.

For example, we have to localize all the areas cultivated that are situated in hilly conditions (Apennines range, north Italy, Mediterranean basin) between a range of 200 to 500 m a.s.l., in which the slope orientation is pertaining to the SE, S and SW quadrants. In this case, the ecotope should represent the xerophitic, warmer site in which olive orchards and vineyards are cultivated, that for convenience we call "wintering sites". In Figure 8.27, a picture of such an ecotope is reported as an example.

This ecotope plays a relevant role in the winters of many small birds (Farina 1987) and this locality can assume a major importance, for example when protection action has to be planned.

The starting point is the input of basic information, in this case:

1. Elevation map (topography)
2. Aspect map (aspect.map)
3. Land use map (cultivation)

Maps 1 and 3 have been created by digitizing existing maps, the aspect map n. 2 has been created by using the "orient" procedure of MacGIS routine for elevation maps.

The model is very simple and obtained using the following steps:

1. select all cells ≥200 and <500 from the topography map and save a new map as a hill
2. select map cultivation from land use and save a new map cultivation
3. run "orient" routine on topography and save a new map orient
4. select from orient values 4, 5, 6 that represent SE, S, and SW orientation respectively and save a new map southern
5. recode assigning value 1 to southern, cultivation and hill and save each map assigning the name "southern.1, cultivation.1, hill.1"
6. use the routine "add" in adding the three maps, then select only locations with a value of 3, this represents the ecotope "wintering site" that we have searched.

This procedure can be simplified and the chrono-sequence changed without modifying the results.

### 8.4.14 Key study 2

The aim of this example is to classify a soil surface in terms of the potential connectivity of a perennial grass cover (*Brachypodium genuense*) for the movement of micromammals like *Pitymys savii*.

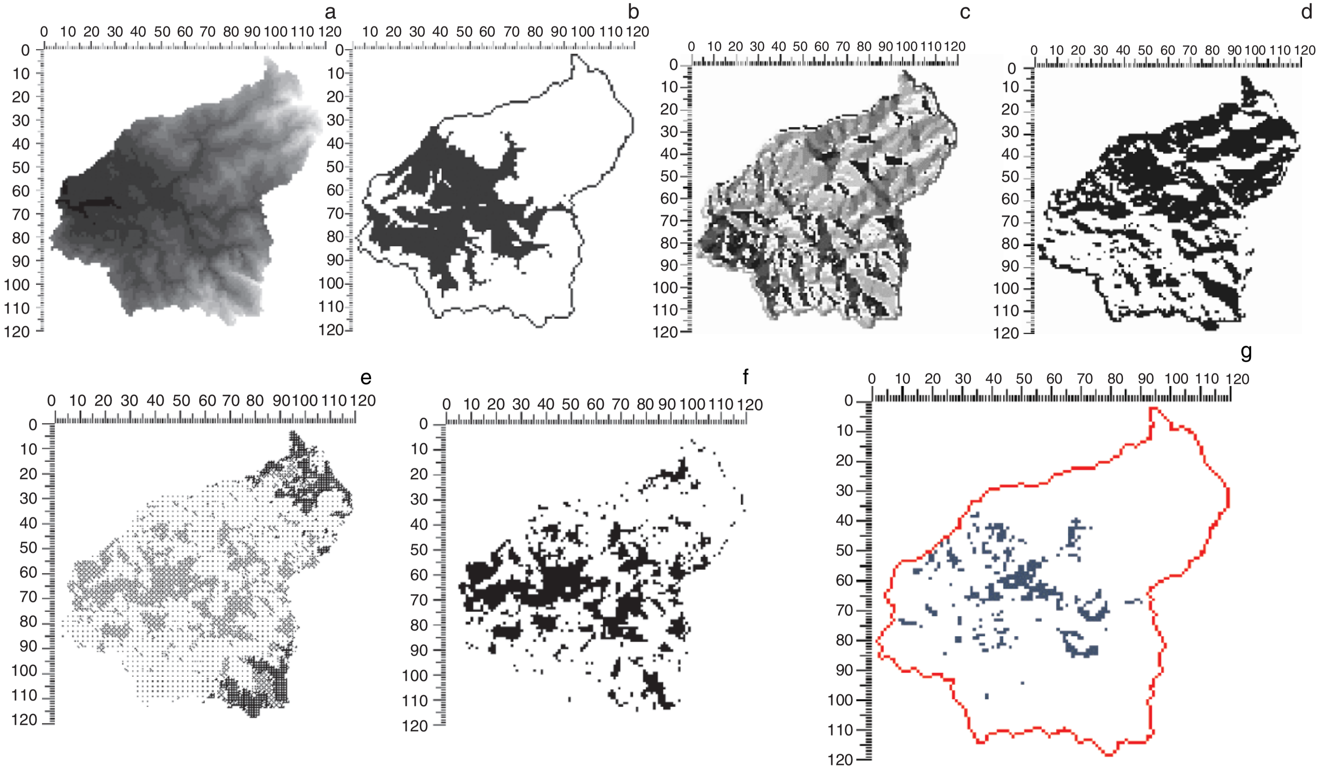


*Figure 8-27*. Data preparation 1:

- Selection from the topography map (a) of the hilly portion of terrain ranging from 200 to 500 m of Aulella watershed (b),
- Selection of SE, S, SW and W aspect of Aulella watershed slopes from orient map (a) in Southern map (b)
- Selection of cultivations (f) from the land cover map (e)
- Calculation of ecotope wintering site(g) adding maps hill.1 + southern.1 + cultivation.1 after their recording with 1 for all not 0 values. The cells with value 3 have a combination of all three maps, then are the selected ecotope (data from Farina 1997).

In this example, the small surface of mountain prairies (Logarghena, Northern Apennines) has been captured using a digital camera (Quick Take ®), suspended from a balloon and switched remotely at an altitude of 30 m (Figure 8.28).

The image was classified by using Dimple® software according to nine land cover types from unclassified to annual grassland, to perennial grassland and shrubs.

The classified image was imported into MacGIS using the routine "import", the ground resolution was .25 cm x pixel.

The category of perennial grassland was isolated and then by using the routine MacGIS "Spread", the distance of each cell from this target land cover was calculated. Ten distance categories were distinguished, using darker grey tones. This last map may be utilized as a basal map for modeling the probability of *Pitymys savii* to find non-hostile habitat when moving for foraging.

## 8.5 REMOTE SENSING IN LANDSCAPE ECOLOGY

### 8.5.1 Introduction

The goal of this chapter is to briefly review the application of remote-sensing techniques to the study of the landscape. For more information on these techniques that are becoming more and more popular and sophisticated, see Johnson (1969).

Remote sensing and GIS are often used coupled with landscape analysis and classification (e.g., Davis & Goetz 1990). For example, the detection of linear structures in human-dominated landscape can represent an important element for landscape description. Goossens et al. (1991) have tested the capacity of the SPOT multispectral imagery of a rural area in Belgium, to detect ecological infrastructures.

Linear structures such as hedgerows, edges, drainage ditches and roads are detected in different measures by the SPOT sensor. The height of the object (tall objects have longer shade), the sun angle (the lower the sun angle, the longer the shade), and the orientation of trees and edges, all play a role in edge detection. Some measures of detectability have been found:

Land blocks with an area <1.2 ha cannot be detected
Land blocks with an area >3 ha are always detected
Land blocks longer than 300 are always detected
Land blocks <120 m long are not detected.

The availability of images captured by satellites or by aircraft along a multispectral reflectance allows a broad possibility of applications of these techniques to landscape.

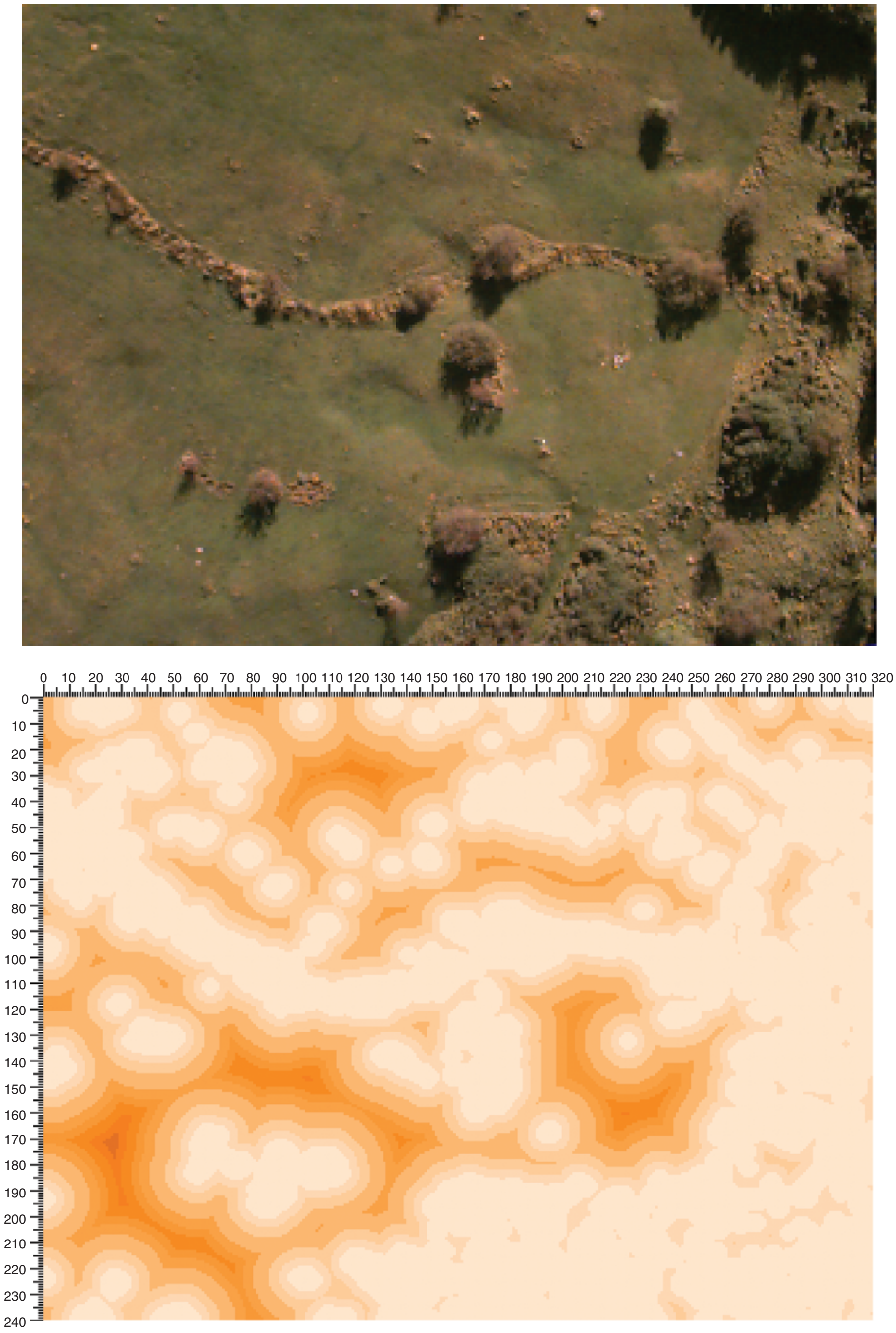


*Figure 8-28*. (a) Low altitude image of Logarghena prairies (Northern Apennines, Italy) taken by a digital camera suspended from a balloon (Spring 1996).

(b) Map of distance (ten categories, from light to dark) from the *Brachypodium* cover after image classification (from Farina, unpublished).

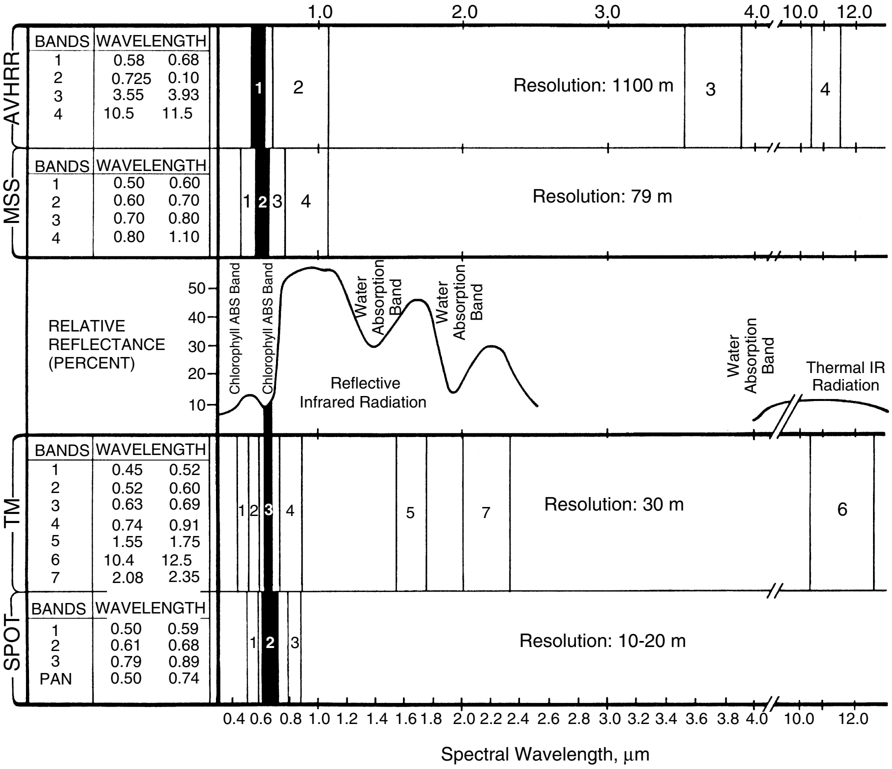
Remote-sensing data can be collected at different spatial and temporal scales, creating a powerful tool to study processes.

Remotely sensed data can be processed and improved through digital techniques also available on inexpensive platforms (Dimple®, Multispec®).

The resolution scale ranges from 10, 20 or 30 m. The Landsat Thematic mapper has a resolution of 30 x 30 m on the ground. SPOT has a 10 x 10 m ground resolution.

In a landscape, each element has a characteristic multispectral response (Figure 8.29).

Hall et al. (1991) has used Landsat Multispectral Scanner (MSS) data (60 m of resolution) to study the boreal forest landscape across a temporal scale of 10 years.



AVHRR

| BANDS | WAVELENGTH | |
|---|---|---|
| 1 | 0.58 | 0.68 |
| 2 | 0.725 | 0.10 |
| 3 | 3.55 | 3.93 |
| 4 | 10.5 | 11.5 |

MSS

| BANDS | WAVELENGTH | |
|---|---|---|
| 1 | 0.50 | 0.60 |
| 2 | 0.60 | 0.70 |
| 3 | 0.70 | 0.80 |
| 4 | 0.80 | 1.10 |

TM

| BANDS | WAVELENGTH | |
|---|---|---|
| 1 | 0.45 | 0.52 |
| 2 | 0.52 | 0.60 |
| 3 | 0.63 | 0.69 |
| 4 | 0.74 | 0.91 |
| 5 | 1.55 | 1.75 |
| 6 | 10.4 | 12.5 |
| 7 | 2.08 | 2.35 |

SPOT

| BANDS | WAVELENGTH | |
|---|---|---|
| 1 | 0.50 | 0.59 |
| 2 | 0.61 | 0.68 |
| 3 | 0.79 | 0.89 |
| PAN | 0.50 | 0.74 |

*Figure 8-29.* Spectral and spatial resolution for the commonest civilian satellites: AVHRR, MSS, TM and SPOT, and the electromagnetic spectral response curve for green vegetation (From Iverson et al. 1989, with permission).

### 8.5.2 Effects of sensor spatial resolution on landscape structure parameters

Remote sensing has been usefully applied to verify the scaling properties of the landscape (Nellis & Briggs 1989; Benson & MacKenzie 1995).

For example, Nellis & Briggs (1989) have used band rationing between Landsat Multispectral Scanner (MSS) and Thematic Mapper (TM) combined with image textural features at three scales. Band rationing was used to estimate and monitor green biomass.

Healthy vegetation reflected 40 to 50% of incident near-infrared energy (0.7 to 1.1 micrometers) and absorbed 80 to 90% of the incident energy in visible (0.4 to 0.7 μm) close to the red region (0.6 to 0.7 μm) part of the spectrum. The ratios between MSS bands 4 to 2 and TM band 4 to 3 (the ratio of near-infrared energy to visible energy) were particularly useful in determining the quantity of biomass or net primary production.

Three scales of resolution were used, 5 m (digitally improved aerial photographs) (spectral resolution of 0.3 μm), 30 m (TM) and 80 m (MSS).

The textural contrast between adjacent pixels was carried out using 0–255 categories of contrast.

Different components of the Konza prairies landscape reacted differently to sensor resolution. Areas of dense patchiness have to be analyzed at a finer scale than the areas burned every four years. In this case, aerial photography and Landsat were preferred to study unburned areas.

Using high resolution digitally enhanced photography it was possible to appreciate the greatest difference in the degree of textural contrast.

In conclusion, the Landsat MSS digital data is less suitable for mapping Konza prairies.

SPOT multispectral high resolution visible (HRV), the Landsat Thematic Mapper (TM) and NOAA, Advanced Very High Resolution Radiometer (AVHRR) were used to compare the change of landscape structure in the northern Wisconsin lake district by Benson & MacKenzie (1995). The landscape parameters used were: % water, number of lakes, average lake area and perimeter, fractal dimension and three measures of mosaic texture (homogeneity, contrast and entropy). For these indices, see the methods in this chapter. These measures were sensitive to sensor resolution moving from 20 m of HRV to 1100 m of AVHRR. For instance, the number of lakes and the percentage of water in the landscape decreases as grain size increases. However, homogeneity and entropy resulted invariantly across the satellite sensor resolution (Figure 8.30).

Considering that the major landscape parameters are sensitive to sensor resolution and that at different resolutions landscape patterns appear or vanish, it would be important to fill the great interval resolution between the TM and AVHRR (30 to 1100) using interpolating procedures.

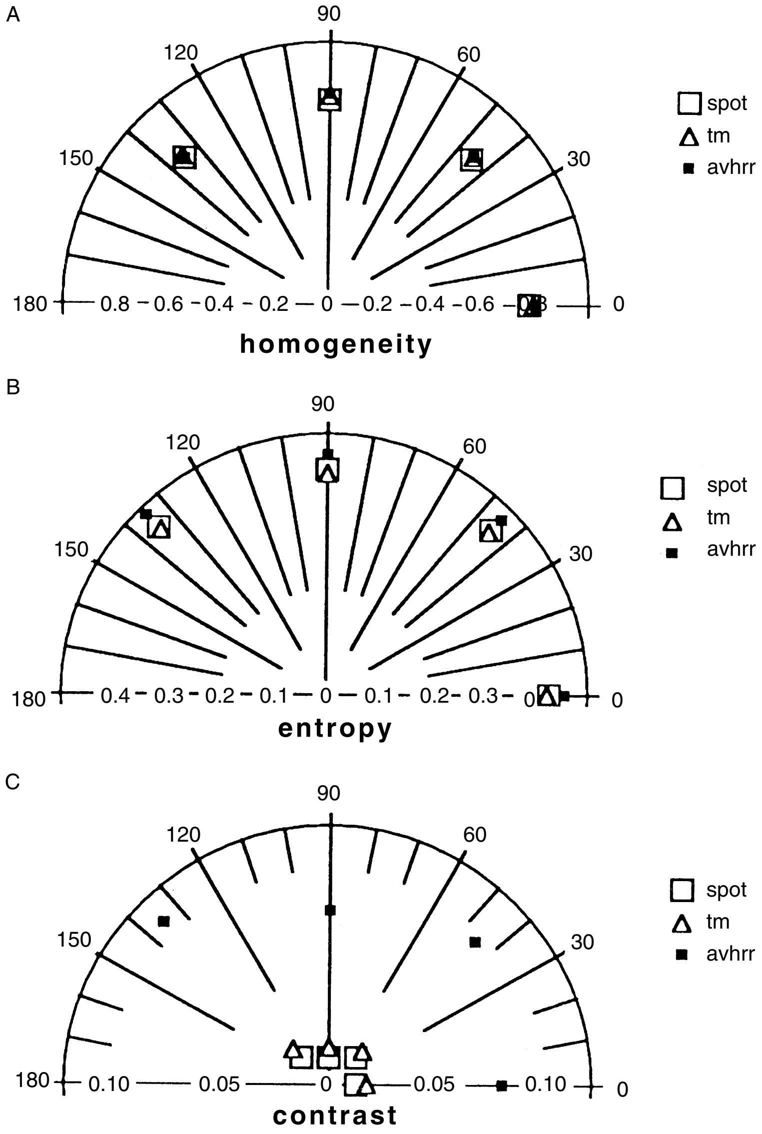


*Figure 8-30*. Texture values for HRV, TM and AVHRR according to the angle of analysis for three texture parameters (a) homogeneity, (b) entropy, and (c) contrast. Only contrast shows any sensitivity to sensor resolution. Angle used for proximity of pixels does not seem to have any effect (from Benson & MacKenzie 1995, with permission).

Scaling the remote-sensing land cover classification is an efficient practice to determine the scaling properties of landscapes. For instance, Moody & Woodcock (1995) have used MT 30 m resolution of Plumas National Forest (California) aggregated into 5 classes of resolution (90, 150, 240, 510 and 1020 m).

The changes in land cover type due to progressive aggregation procedures were tested using five independent variables: mean patch, mean interpatch distance, Shannon index, variance mean ratio and initial proportion.

Generally, the decrease of resolution due to pixel aggregation introduces a large proportion of errors. These errors strongly influence the reliability of large-scale modeling. Understanding the behavior of spatial data when they are aggregated is useful for preserving the information.

Simmons et al. (1992) have used satellite imagery to evaluate the ecological scale, applying the methods used by Carlile et al. (1989) (see the chapter on scaling).

### 8.5.3 Remote sensing and landscape boundaries

Boundaries, also defined as transitional zones between landscape units, are fundamental structures in any landscape (see chapter on Ecotones).

Metzger & Muller (1996) propose new boundaries indices using remote-sensing data (Table 8.9).

*Table 8-9*. Indices used to calculate boundary proportion and complexity (from Metzger & Muller 1996, with permission).

**A. Indices of landcover and boundary proportion**

$pi = Ai/A$ Proportion of land cover where: Ai is the area of landcover i and A the area of landscape

$qi = Bi/B$ Proportion of landcover boundary i where: Bi is the boundary area of landcover i, B is the landscape boundary area

$Fi = Bi/Ai$ Shape index or proportion of boundary area in landcover i

$F = B/A$ Landscape fragmentation index or proportion of boundary area within the landscape

**B. Indices of landcover boundary complexity**

$Ci = Bci/Ai$ Proportion of convergency points (or coverts) in landcover i where: Bci is the area of coverts in landcover i

NBi Number of boundary types in landcover i

$HBi = \sum_{K=1}^{NBi} -qki \times \log_2 qki$ Boundary diversity index in landcover i of each boundary type k

**C. Indices of landscape boundary complexity**

$C = Bc/A$ Proportion of convergency points (or coverts) in landscape where: Bc is the area of coverts in the landscape

NB Landscape boundary richness index, i.e. the sum of the number of simple contacts (points where two landcovers converge) and coverts (points where three or more landcovers converge)

$HB = \sum_{K=1}^{NB} qk \times \log_2 qk$ Landscape boundary diversity index where: qk is the boundary area proportion in the landscape of each boundary type k.

Using a Landsat Thematic Mapper image of Jacaré-Pepira basin (State of Sao Paulo, South-East Brazil) a supervised classification was made using red (TM3, near infrared (TM4) and shortwave-infrared (TM5) spectral bands with the normalized difference vegetation index (NDVI=(TM4-TM3)/(TM4+TM3)).

After the land cover classification, the boundary pixels were extracted, then dilated, placing the same pixel to each side of boundary pixels. The dilated boundaries are then added and boundary types extracted for each land cover as a combination of the three types. For example, the value 6 is the result of 2+4 land cover types, 12 is the result of 8+4, etc.

This approach clearly showed the importance of boundary analysis to interpret landscape complexity. Landcover boundary diversity is significantly related to landcover shape. Elongated riparian units have the highest value for boundary diversity and covert proportion indices. Shape, richness, diversity and covert proportion are important descriptors of landscape complexity.

### 8.5.4 Forest ecology and remote sensing

The first civilian earth-observing satellite was launched in 1972. From that time to the present, enormous progress has been made in remote sensing, especially in the field of land cover classification. Due to the coarse grain of Landsat TM, MSS and AVHRR, only large areas can be usefully classified. Here, landscape ecology finds an invaluable tool in remote sensing producing sophisticated information in natural as in human-modified landscapes. The coupling of image analysis to GIS facilities, then incorporating spatial referenced data as topography, has strongly improved the quality of the numerical and graphic output (Figure 8.31 and Table 8.10).

Mostly used in land cover classification, the remote sensing approach is moving towards the landscape changes. Due the recent history of this technique, comparisons are restricted to two decades, but future perspectives are strongly predicted.

The procedure to classify a satellite multiband image is described in detail in many software handbooks. But in extreme synthesis, two different approaches are available to classify an image. First an automatic a priori unsupervised classification based on differences in the spectral characters of the pixels. After the classes are generated, it is necessary to assign meaning to the classes (converting classes to landcover type). The sensor most accurate in forest mapping seems to be the TM sensor, especially bands 1, 5 and 7.

The second method called "supervised classification" consists in the creation of training sets, selecting aggregations of pixels in which we recognize a distinct land cover or a vegetation type. The image will be classified according to the selected training sets.

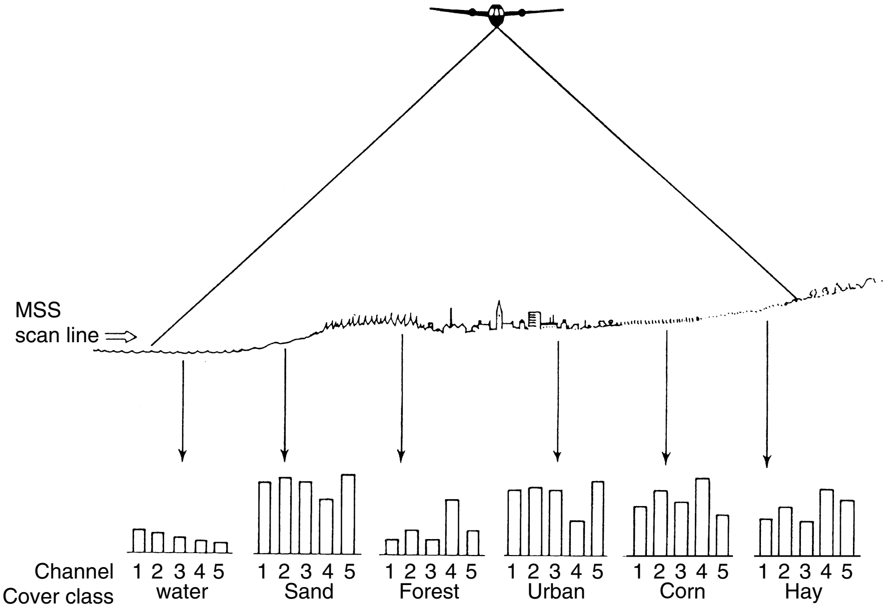


*Figure 8-31*. Spectral attributes belonging to different land cover types. Band 1, blue; band 2, green; band 3, red; band 4, near-infrared, band 5, thermal-infrared (from Lillesand & Kiefer 1987, with permission).

## 8.5.5 Landscape classification using remote sensing

Remote sensing allows one to classify land cover types, often with good reliability (Figures 8.27, 8.31). But higher order patterns in the land cover mosaic that represent different landscape types cannot be immediately recognized using this technique. Haines-Young (1992) has coupled TM and MSS digital processes of selected areas in south east Wales to the program TWISPAN.

Haines-Young grouped the land cover combination 1 km x 1 km cells of the National Grid into landscape classes finding a good correspondence with ITE

Table 8-10. Main satellite types, spatial resolution and temporal coverage (from Cracknel & Hayes 1993, with permission).

| System | | IFOV (Instantaneous Field-of-View) | Repeat coverage |
|---|---|---|---|
| SPOT | Multispectral | 20 m | Days-variable |
| | Panchromatic | 10 m | Days-variable |
| LANDSAT | MSS | 80 m | Several days |
| | TM | 30 m | Several days |
| NOAA | AVHRR | ~ 1km | Few hours |
| METEOSAT | | ~2.5 km | 30 minutes |

(Institute of Terrestrial Ecology) Land Classes for Great Britain and the Agricultural (Jane) Census statistics for England and Wales.

To classify the landscape, the classified images were geometrically corrected using a nearest neighbor algorithm to the UK Ordnance Survey National Grid.

In this way, it is possible to include the landscape type in the general framework of remote sensing.

### 8.5.6 Calibration center concept

The combined use of TM and AVHRR was tested by Iverson et al. (1994) at two locations (Illinois and Smoky Mountains). The TM data were used to classify a smaller area (calibration center) into forest/non-forest. The combination of TM and AVHRR data allows a better interpretation of AVHRR data. The unsupervised classification technique was used to classify forest/non-forest TM data at a resolution of 30 m. The classification was verified using aerial photographs.

The AVHRR pixels (1 km resolution) were superimposed onto TM pixels (30 m resolution). 154 AVHRR pixels, each of which contained 1,369 TM pixels for the Illinois area, and 99 AVHRR pixels with 871 TM pixels. A regression analysis was carried out to determine the best correlation between spectral characteristics of the AVHRR data and the TM data.

AVHRR alone can underestimate or overestimate forest cover. The TM calibration improves the discriminant efficiency of AVHRR. The efficiency of this methodology largely depends on the soil topography and on the reflectance of the vegetation. Conifer and broadleaf forests have different behavior and calibration must be repeated for the two conditions to avoid misclassification.

## 8.6 GLOBAL POSITIONING SYSTEMS (GPS)

Recently, we were able to localize features of interest using the Global Positioning System (GPS). This system, born for missile and airplane automatic navigation, is based on radio information of the field position calculated by a cluster of satellites. Practical use of GPS has been presented in the ornithological studies of bird communities (Farina 1997). The positions of birds introduced by an operator in a datalogger were transferred to a computer for processing (Figure 8.32). This information at the end was inserted into a GIS for mapping and spatio-statistical elaborations. The Global Positioning System is a satellite-based positioning system operated by the US Department of Defense (DoD).

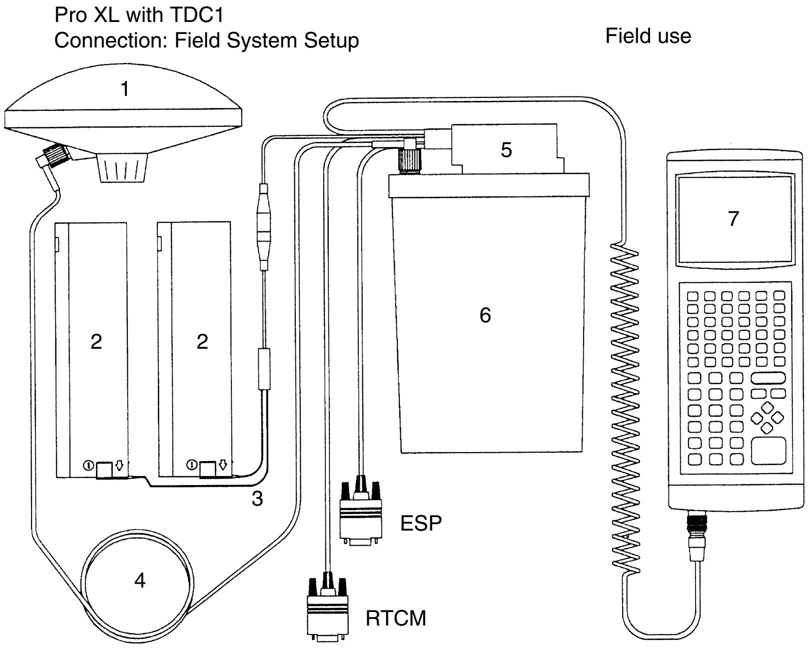


*Figure 8-32*. Technical equipment of a Rover Station ProXL with TDC1.
1= Compact dome antenna, 2= Camcorder batteries, 3=Dual battery cable, 4= Antenna cable, 5= TDC1/ProXL multiport cable, 6= 12-channel ProXL receiver, 7= TDC1 4MB data collector, ESP= External Sensor Port cable, RTCM= Radio Technical Commission for Marine Services, real-time differential correction cable (Trimble Navigation 1994, with permission).

GPS one allows one to collect information about the geographical position of any location, using a network of satellites.

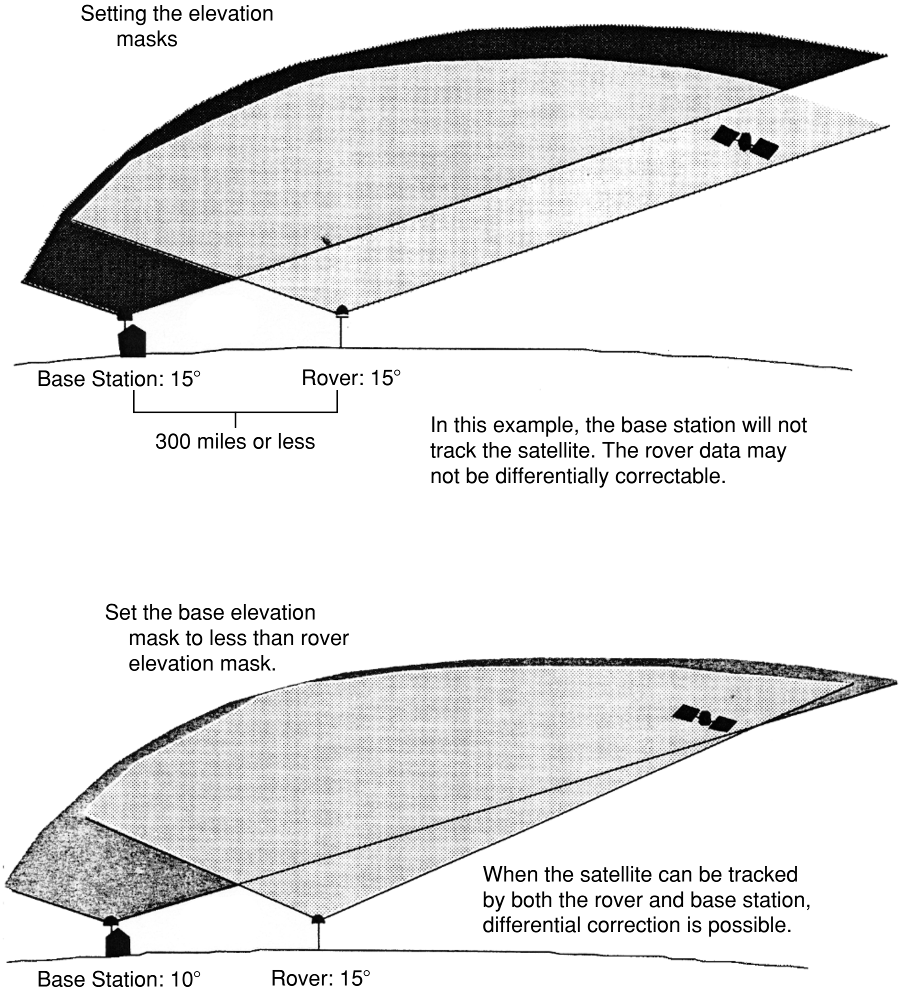
When fully operative, the information is covered by 24 satellites NAVSTAR (Navigation Satellite Time And Ranging) in 12-hour orbits at an altitude of 20,200 km.

The system was started in 1973 and the first satellite was launched in 1978. Civilian use, very expensive, was available in 1983. Actually, the system is less expensive depending on the accuracy requested. The development of this technology, especially on receivers, allows the precision of 1 cm working, also below dense tree coverage.

The GPS system works by using the satellite trilateration, measuring the distance between satellites, calculating the accurate timing, knowing where a satellite is in space and for correcting ionospheric and tropospheric delays.

The accuracy of the system depends on the equipment used and by the processing methods. For security reasons, the DoD can degrade the accuracy with

Selective Availability (SA). SA degrades the information used by civilian navigation receivers, miscalculating their position by hundreds of meters. To correct this bias a posteriori, differential corrections can produce an accuracy from 2 to 5 m (Figure 8.33).



In this example, the base station will not track the satellite. The rover data may not be differentially correctable.

When the satellite can be tracked by both the rover and base station, differential correction is possible.

1° per 100 km distance between base and rover.

*Figure 8-33*. Representation of the interconnections between base station and rover to allow a differential correction. In A, the elevation mask of the base station and of the rover is the same and the base station cannot track the satellite. In B, the elevation mask of the rover is narrower then the mask of the base station. In this case, the satellite can be tracked by both the rover and base station. Elevation Mask is the elevational angle above the horizon (from Trimble Navigation 1994, with permission).

Another source of inaccuracy is produced by Anti-Spoofing (A/S) affecting dual frequency receivers.

The differential correction for SA is a technique that employs two receivers: one basic station and one (or more) remote receiver or rover. The position of the basic station is known with high precision so it is possible to correct the biases introduced by SA. Commercial software is available to carry out this procedure.

To be operative, a rover should have a large portion of sky visible and the position of satellites with a constellation geometry. The constellation is a group of three or four satellites used by the receiver to calculate a position. Four satellites are necessary for a 3D position (latitude, longitude, altitude and time), a 2D position (latitude, longitude and time) necessitates three satellites.

The quality of a position is indicated by the DOP (Dilution of precision) value that appears on the receiver. The DOP value depends on the geometry of the satellites, there are four types of DOP:

Position (PDOP) horizontal and vertical measurements (lat, long, alt)
Horizontal (HDOP) horizontal measurements (lat, log)
Vertical (VDOP) altitude
Time (TDOP) clock offset.

PDOP below 4 gives excellent position, between 5 to 9 acceptable, >9 poor.

It is possible to set the receiver to store positions only below a PDOP value, generally fixed at 6. Some receivers may require a PDOP mask with a value below 4 to achieve submeter accuracies.

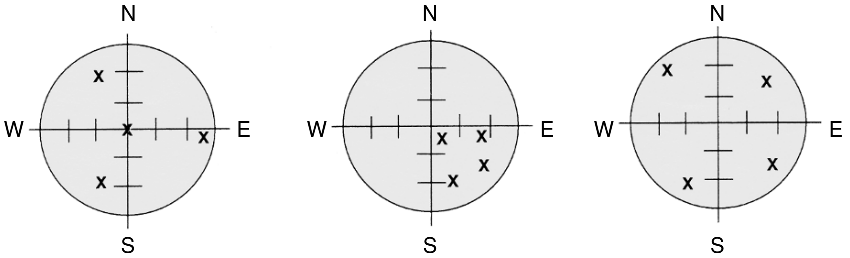
To achieve the best results, it is important to known the satellite position in advance. An Almanac can be recorded automatically from satellites on the receiver (Basic station or rover). In this way, some software can calculate for any position the value of PDOP and/or separately HDOP, VDOP and TDOP (Figure 8.34).

## 8.6.2 The use of GPS in landscape ecology

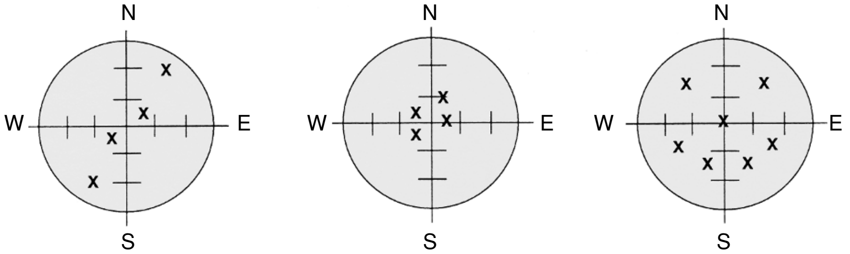
GPS has great potentialities in landscape ecology, like in many other geography-related disciplines.

GPS may be used directly in the field, on cars and airplanes and helicopters for collecting point, line and surface features. A Data Dictionary prepared *ad hoc* for each project can be used in the datalogger to facilitate data input. Extensively employed in forest and agricultural mensuration, it has also been used recently to capture the position of animals (Farina 1994, 1997), but also in archeology and anthropology (Figure 8.35).

The geographical position of an event such as a bird encounter, a bird call or other behaviours are recorded contemporarily to any features



1. Good PDOP, HDOP, VDOP 2. Poor PDOP, HDOP, VDOP 3. Poor PDOP, good HDOP, poor VDOP



4. Poor PDOP, poor HDOP, good VDOP 5. Poor PDOP, poor HDOP, good VDOP 6. Have a good DOP

*Figure 8-34*. Geometry of satellite constellation and Dilution of Position (DOP) values for Position (PDOP) (longitude, latitude and altitude), Horizontal (HDOP) (latitude and longitude), Vertical (VDOP) (altitude), Time (TDOP) (clock offset). The most accurate satellite geometry is illustrated in position 1. when a satellite is directly overhead and the other three are evenly spaced around the horizon (Trimble Navigation 1994, with permission).

we like to add. Then this information is transferred into a desk computer and, using a specific software, the differential correction and other processes are carried out.

Data can be exported in a different format and for any purpose. After processing, data can be handled as a GIS, each location can be measured as the distance from other features, and different files can be merged together with an automatic rescaling of the video images.

The GPS methodology has been a revolution in the field of bird community ecology, boosting the census techniques finally independently from the low resolution of topographical maps. New receivers can actually receive satellite signals also under a dense vegetation cover, expanding in this way the range of possible applications.

GPS can be used to rectify aerial photographs, low-altitude oblique photographs, and mapping vegetation patches on the ground with an accuracy of 5m after differential correction.

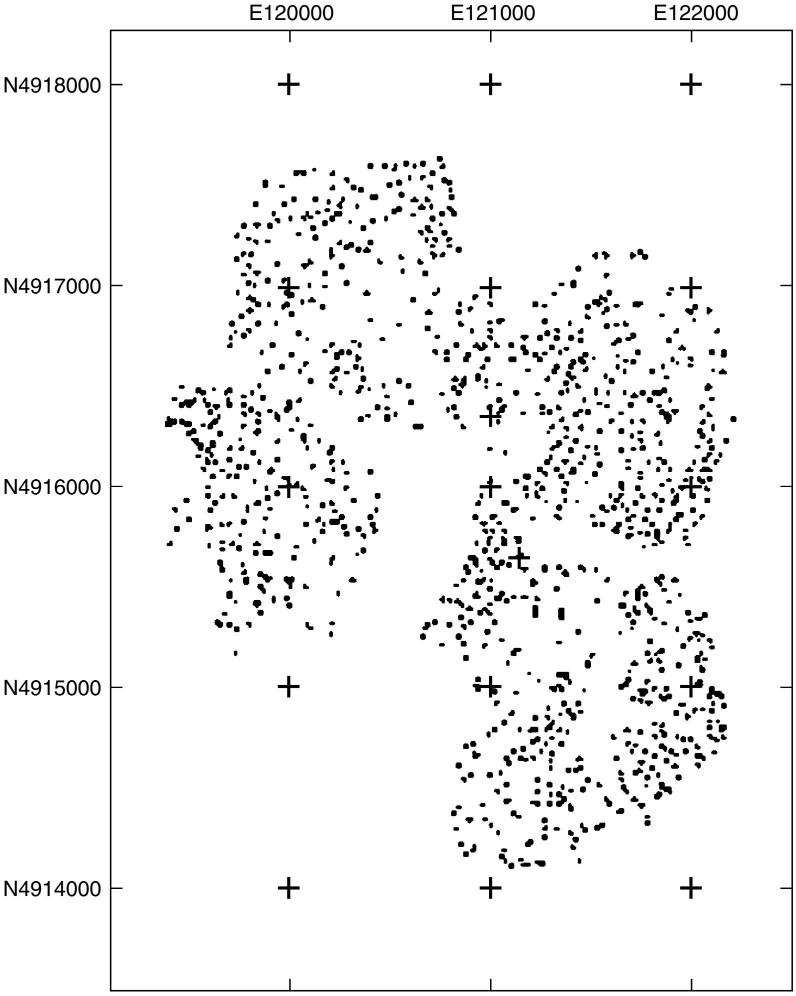


*Figure 8-35*. Example of output of field data (charcoal plaza) collected by using a GPS rover along a random transect in a mountain beech forest (La Nuda Mt., northern Apennines) (from Farina, unpublished).

## 8. 7 SPATIALLY EXPLICIT POPULATION MODELS (SEPM) TO DESCRIBE POPULATION PATTERNS IN A LANDSCAPE

### 8.7.1 Introduction

When a population in a landscape is reduced in number and confined to a small area, the risk of local extinction may be high. Unfortunately, this condition is becoming common in fragmented and human-disturbed landscapes.

To study the model of spatial movement of a population in a landscape a cellular automaton can be applied that is a cartesian grid of identical cells, each of these has a finite number of states or attributes. In the model, the updating process is referred to all cells according to the state of neighboring cells. In landscape ecology the cartesian grid cells represent an area of the land surface and cell states correspond to landscape features.

To study animal populations in heterogeneous landscapes, spatially explicit population models seem to be very promising tools. In fact, these models incorporate the complexity of the real-world landscape (topological and chronological components). One advantage in using these models is to investigate the responses of organisms to a broad scale of ecological processes. Changes in land use and climatic changes modify the environmental conditions which the organisms are facing and these processes often create intriguing conditions that cannot be studied with traditional techniques.

A spatially explicit approach is very efficient for modeling large-scale disturbances such as fires in ecosystems. To apply these models in an efficient way, it is necessary to create a strict relationship between modelers and field ecologists.

A spatially explicit model is structured in such a way that the precise location of each element (organism, population, habitat patch) is known and compared with the landscape features (corridors, edges, woodlots, rivers, fields, forests, etc.). Every element in these models, can be compared with the changes occurring in landscape path composition and spatial arrangement. To build such models, it is necessary to define the grain size of the landscape (individual patch cell). Habitat patches may have the dimensions of a cell but generally are composed of more cells with the same characters. The extent of landscape considered generally spans from micro to meso-scale (<1 ha to104 km).

The type of landscape used in these models can be real or artificial. In the first case, few land uses or other characters, are preferable. The artificial landscape is used to simulate the responses of species.

Models can be individually based or population based. In the first case, the position of each individual at an annual step or daily step is simulated. At the annual scale, breeding, dispersal and mortality are considered. At the daily scale, foraging, growth, predator avoidance and roosting selection can be monitored.

The population models are generally applied to invertebrates and mammals that have consistent populations. In this case, metapopulations models can be incorporated into SEPMs.

SEPMs have the capacity to incorporate the dispersal rules of individuals across a landscape although the species-specific perception of the landscape is little known.

Other difficulties can emerge when the scale is enlarged and the sensitivity of a species to some character of the landscape can change.

In a real-world landscape, the distibution of resources changes over time and space and organisms react to this. The impossibility of manipulating "large" landscapes can be overcome by using organisms living in micro-landscapes that can be easily manipulated.

SEPM can be used to design natural reserves and predict the persistence of a species according to the landscape element. These models, parameterized according to a species' life history, can verify the adequacy of existing reserves.

SEPM can serve as a bridge between spatial ecology and the genetics of populations by exploring the gene movements into a population (metapopulation). Another interesting perspective is the combination of models predicting forest dynamics due to global change with the reactions of animals to these environmental changes. SEPM can include also nonbiological parameters like forest economics.

The model proposed by Darwen & Green (1996) has considered no landscape-obstacle for population diffusion at the start of simulation. Although there simulated available space around the population, an absence of predators and a lack of any other cause of extinction, extinction still occurred in the model. This represents a warning point usable for species conservation. If the population is too small and occupies a small area, it suffers from a high risk of extinction.

## 8.7.2 A spatial patch dynamic model

Wu & Levin (1994) have proposed a model based on a spatial patch dynamics platform to study dynamics at local and landscape scales, useful to study the age- and size-structured disturbance patch population and to assess the manner in which local disturbances and patch dynamics affect vegetation pattern at the landscape scale (Figure 8.36).

These authors have studied the Jasper Ridge Serpentine Grassland. This area, due to the particular condition of soil deficiency of Ca:Mg ratio and high concentration of heavy metals, has a specific grass and forb cover with a very low abundance of non-native plants. Pocket gophers (*Thomomys bottae* Mewa) is the major disturbance source. This species burrows in the soil and creates mounds of bare soil. Most gopher mounds are created in April and July and about 20% of the entire area is turned over by gopher activity each year. This mound can be compared with forest gaps in developing a dynamic patch.

The recover phases are: nudation, dispersal and colonization, plant establishment, intraspecific competition and achievement of the pre-disturbed state.

The grassland landscape is represented by a patch mosaic of gopher mounds of different age.

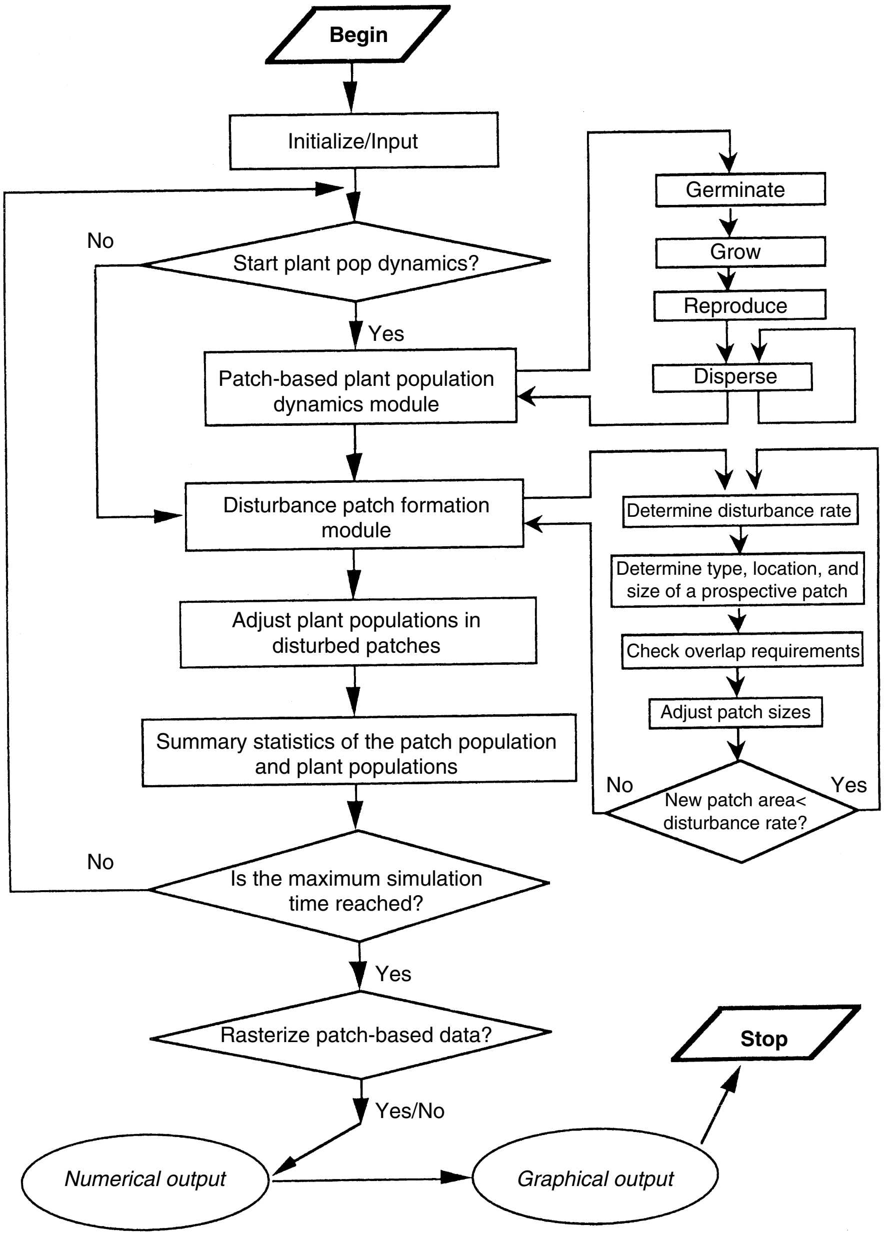


*Figure 8-36*. Flow chart of the spatial dynamic model PatchMod (from Wu & Levin 1994, with permission).

These models allow testing of the conceptual framework of patch dynamics focusing on spatial heterogeneity, transient dynamics and relationships among hierarchical levels.

This model was composed of two parts: a disturbance patch demographic model and a multi-species population dynamic model.

The first component of the models considered the shapes, sizes and types of patches, their spatial distribution and the disturbance rate. The Multiple-species population dynamic model took into account a patch-based multiple-species plant population dynamic model and the effect of patch age in plant demography parameters (Figure 8.37).

Other examples of spatially explicit models have been presented by Liu et al. (1995). These authors have elaborated a model called ECOLECON.

This ecological-economic model simulates animal population dynamics and economic revenue, according to different forest landscape structures and timber management. It is a second-generation model built on BACHMAP, a spatially explicit model of population dynamics of Bachman's Sparrow.

Pulliam et al. ( 1992) have adopted the MAP (Mobile Animal Population), a spatially explicit population model to study habitat preferences of Bachman's Sparrows (*Aimophila aestivalis*), a threatened bird living in pine woods in the south-eastern United States (Figure 8.38).

This species is particularly sensitive to habitat management.

Three categories of variables have been incorporated into this model:

(a) Landscape variables that take into account habitat abundance and the spatial arrangement of habitat patches.
(b) Habitat-specific demographic variables (reproductive success and survival rate).
(c) Behavioral variable that describes the dispersal habit of the species.

The model was built using 20 age classes, old growth category and clearcut. Model simulation was made for a period of 105 yrs (five harvest rotations).

Patterns of abundance and distribution of a population may reflect not only the current landscape characteristics but also the characteristics of the past landscape.

A further development of spatially explicit individually-based models is the creation of expert systems able to predict the complex behavior of species. For instance, Carter & Finn (1999) have developed an expert system, called MOAB, able to explore the influence of landscape patterns on animal movements and foraging behavior. MOAB is a raster-based geographic information system (GIS) in which in each cell composing the matrix are stored the habitat type, resources and individual present and the history of events that occurred. Such an expert system has been described in terms of the superiority of the stochastic models by these authors.

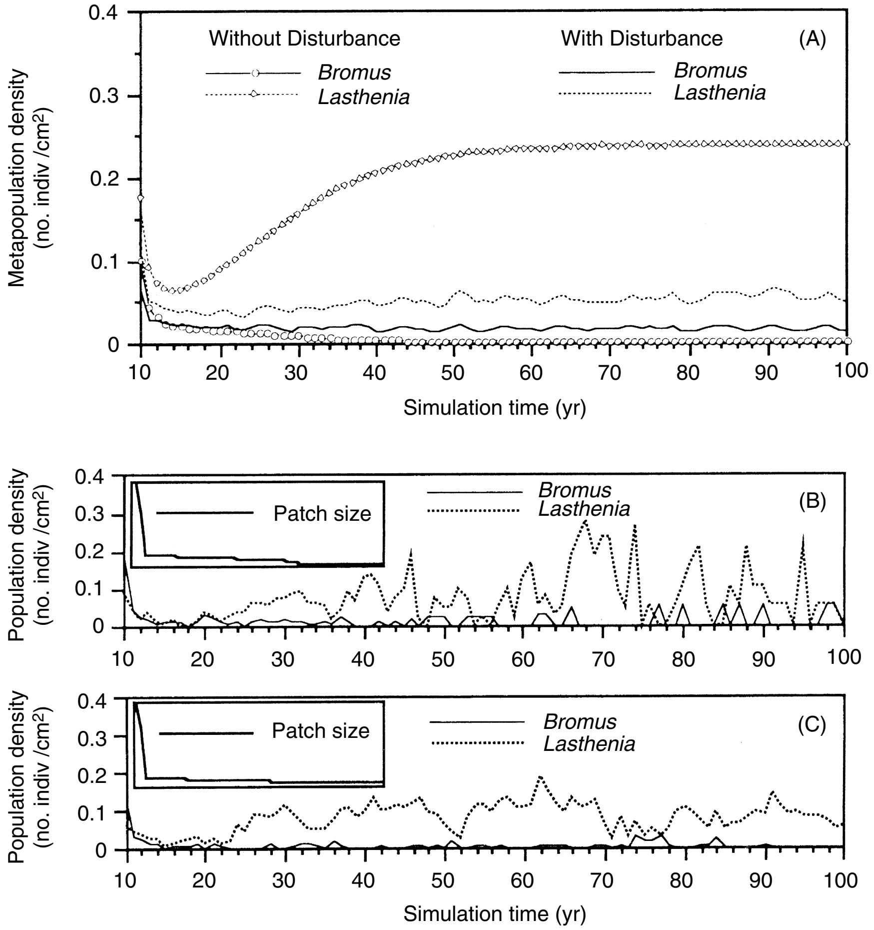


*Figure 8-37*. Simulation dynamics from 10 to 100 yrs at landscape scale (A) and (B,C) at patch scales of two competing species *Bromus mollis* and *Lasthenia californica*. B and C are chosen as arbitrary examples. In case (A) low or absent disturbance, a competitive exclusion is evident, but in the presence of disturbance (Gopher mounds) the local population presents high fluctuations for both the species. New disturbance patches favor the persistence of *Bromus mollis* because this species has a good dispersal (large portion of seeds compared with *Lasthenia californica*). This phenomenon can also be observed in Mediterranean upland grasslands mown and grazed. The disturbance coupled with enhances species diversity reduces the competitive exclusion effect (from Wu & Levin 1994, with permission).

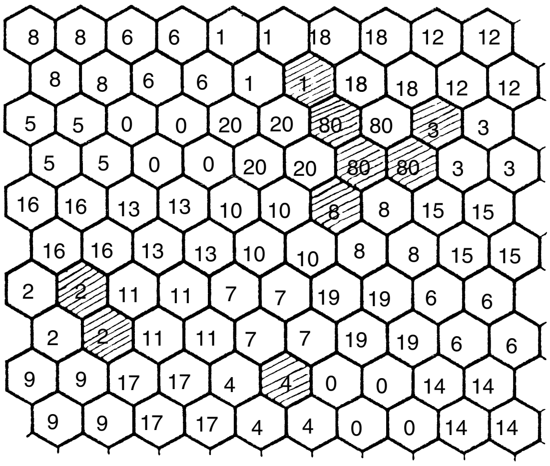


*Figure 8-38*. Hexagonal cells comprise a simulated landscape in which the number in the cells indicates the age of the stand (1-20 yrs harvest rotation). 80= mature stand. Shaded hexagons are occupied by Bachman's sparrow (*Aimophila aestivalis*). Hexagonal cells are used because densely packed bird territories have approximately an hexagonal shape and an extensive border that allows us to model dispersal in all directions (from Pulliam et al. 1992, with permission).

*Box 8.1*. Program to calculate patch characters. This routine has been prepared in Basic.

```
REM MPC  MEASURE OF PATCH CHARACTERISTICS
REM Program to calculate:
REM 1. First Shape Index Perimeter L/S ratio
REM 2. Second Shape Index Corrected Perimeter/Area CORR =(.282*L)/√S
REM 3. Third Shape Index Related circumscribing circle RCC=2*(area/pi)1/2/longest-axis
REM 4. Fourth Shape Index S1 1/Ni* (Li/Si) Ni =number of patches of category in a map
REM 5. Fifth Shape Index S2=1/Ni* (Li/4 √Si)
REM data input
REM S = Patch area
REM Si = Patch area of the category i
REM L = Perimeter
REM Ax = Longest Axis
REM that.file is the name of your data file

OPEN “I”, #1, “that.file” ‘your file data
100 if eof(1) then  end: goto 1000
cc=cc+1
INPUT #1, area, perimeter, laxis

a(cc)=area: p(cc)=perimeter: ax(cc)=laxis

goto 100
1000
FOR j= 1 TO cc
ls=p(j)/a(j)
corr=(.282*p(j))/SQR(a(j))
RCR=2*SQR((a(j)/3.14))/ax(j)
tot=tot+ls
p(j)=p(j)/4
a(j)=SQR(a(j))
tot1=tot1+p(j)/a(j)
PRINT USING "##.##"; “First shape index”; ls
PRINT USING "##.##"; “Second shape index”; corr
PRINT USING "##.##"; “Third shape index ”; RCR
NEXT j
S1=1/(cc*tot): ‘ Fourth shape index
S2=1/(cc*tot1): Fifth shape index
PRINT USING "##.##"; “Fourth shape index”; S1
PRINT USING "##.##"; “Fifth shape index”; S2

END
```

Box 8.2. Program to calculate the number and relative importance of cover types, Shannon Diversity, Dominance Index and Inverse Simpson Diversity. This routine has been prepared in Basic.

```
REM diversity routine
REM This routine calculates:
REM 1. Number of cover types: land cover, vegetation, others
REM 2. Relative abundance of cover types
REM 3. Shannon diversity
REM 4. Dominance index
REM 5. Inverse Simpson Diversity
DIM cod1(100), cod2(100)
REM input file, as sequential file produced by exportation from MacGis
REM using the routine export in text format
REM then with Word the spaces between values are filled with a coma
REM the file is saved as text and it is ready to be read by this routine

OPEN "I", #1, "that.file

100 IF EOF(1) THEN GOTO 1000

INPUT #1, A
cod1(A)=cod1(A)+1

GOTO 100
1000 ' number of land uses
FOR l= 1 TO 100
IF cod1(l) ><0 THEN tot=tot+1
NEXT l
PRINT  "Number of categories"; tot
FOR l= 1 TO tot
total=total+cod1(l)
NEXT l
FOR l= 1 TO tot
cod2(l)= cod1(l)/total
cod3(l)=cod2(l)*LOG(cod2(l))
PRINT l, : PRINT USING "#.###";cod2(l)
NEXT l
FOR l= 1 TO tot
h=h+cod3(l)
simpson=simpson+cod2(l)*cod2(l)
NEXT l
PRINT "Shannon diversity", : PRINT USING "#.###";-h
PRINT "Inverse Simpson",: PRINT USING "#.###";1/simpson
PRINT "Dominance",:PRINT USING "#.###";LOG(tot)-ABS(h)
```

*Box 8.3*. Program to calculate Contagion Index. This routine has been prepared in Basic.

```
REM CONTAGION ROUTINE
REM this program has been written in Basic
REM for a matrix of 40×40 cells. You can expand the matrix according your needs
REM The contagion has been calculated for 7
Input “Number of rows”; YY
Input “Number of columns”; xx
Input “Number of land uses”;nlu
DIM cod(yy+1,xx+1), contagion(nlu,nlu)
l=1
OPEN "I", #1, "that.file

100 IF EOF(1) THEN GOTO 1000
INPUT #1, a
cod1(a)=cod1(a)+1
k=k+1
cod(l,k)=cod(l,k)+a
IF k=XX THEN k=0 :l=l+1
GOTO 100
1000 '
FOR j= 1 TO nlu
PRINT j
 FOR k= 1 TO YY
FOR l= 1 TO XX

IF cod(l,k)=j THEN GOSUB 3000

NEXT l
NEXT k
NEXT j
FOR i= 1 TO nlu
FOR l= 1 TO nlu
'
pi(i,l)=pi(i,l)+contagion(i,l)/cod1(i)
IF pi(i,l)><0 THEN tot=tot+ pi(i,l)*LOG(pi(i,l))

NEXT l
NEXT i
PRINT "Contagion" , :PRINT USING "##.###"; 2*LOG(nlu)+nlu
END
3000 '
IF cod(l,k+1)><cod(l,k) THEN contagion(j,cod(l,k+1))=contagion(j,cod(l,k+1))+1
IF cod(l,k-1)><cod(l,k) THEN contagion(j,cod(l,k-1))=contagion(j,cod(l,k−1))+1
IF cod(l+1,k)><cod(l,k) THEN contagion(j,cod(l+1,k))=contagion(j,cod(l+1,k))+1
IF cod(l−1,k)><cod(l,k) THEN contagion(j,cod(l-1,k))=contagion(j,cod(l−1,k))+1:
RETURN
```

*Box 8.4*. Program to calculate ASM (Angular Second Moment), IDM (Inverse Difference Moment) and CON (Contrast). This routine has been prepared in Basic.

```
REM This routine finds the value
REM of ASM Angular Second moment and IDM Inverse Difference Moment
INPUT "col"; col: ‘Column
INPUT "row"; row: ‘Row
INPUT "land cover type"; lct
DIM cod(row+1,col+1), p(lct+1,lct+1), pi(lct+1, lct+1)
l=1
OPEN "I", #1, "that.file
100 IF EOF(1) THEN GOTO 1000
INPUT #1, a
k=k+1
cod(l,k)=cod(l,k)+a

IF k=col THEN k=0 :l=l+1
GOTO 100
1000 '
 FOR k= 1 TO col
FOR l= 1 TO row
p(cod(l,k),cod(l,k+1))=p(cod(l,k),cod(l,k+1))+1
p(cod(l,k),cod(l,k-1))=p(cod(l,k),cod(l,k-1))+1
p1(cod(l,k),cod(l,k+1))=(cod(l,k)-cod(l,k+1))
p1(cod(l,k),cod(l,k−1))=(cod(l,k)-cod(l,k-1))
NEXT l
NEXT k
FOR i= 1 TO lct
FOR l= 1 TO lct
cod1=cod1+ p(i,l)
NEXT l
NEXT i
FOR i= 1 TO lct
FOR l= 1 TO lct
pi(i,l)=pi(i,l)+(p(i,l)/cod1)*(p(i,l)/cod1)
asm=asm +pi(i,l)
p2(i,l)=p1(i,l)^2
IDM=IDM+ p(i,l)/cod1*(1/(1+p2(i,l)))
CON=CON+p(i,l)/cod1*p2(i,l)
NEXT l
NEXT i
PRINT "ASM", :PRINT USING "##.## ";asm
PRINT "IDM", :PRINT USING "##.## ";IDM
PRINT "CON", :PRINT USING "##.## ";CON

END
```

*Box. 8.5.* Program to calculate the Lacunarity Index. This routine has been prepared in Basic.

```
REM LACUNARITY ROUTINE
REM Input information on land cover (Code), Box size (R) and Matrix size (W)
REM W= Number of columns x Number of rows
INPUT code of land use or vegetation
INPUT "Box size"; R
INPUT "Matrix size"; W
REM Dimension of array: cod, n, n1, n2, n3
REM cod=
REM n=
REM n2=
REM n3=
DIM cod(W,W), n(R^2), n1(R^2), n2(R^2), n3(R^2)
l=1
REM prova.txt is a sequential file in which data are in the format:
REM a1,a2,a3
OPEN "I", #1, "that.file
100 IF EOF(1) THEN GOTO 1000
INPUT #1, a: ‘Reading data in the file
IF a><code THEN a=0: ‘selection of land cover type
IF a=code THEN a=1
k=k+1
cod(l,k)=cod(l,k)+a
IF k=W THEN k=0:l=l+1
GOTO 100
1000 '
nr=(W-R+1)^2
FOR l= 1 TO W-(R-1)
FOR k= 1 TO W-(R-1)
FOR i= 0 TO R-1
FOR j= 0 TO R-1
TOT=TOT+cod(l+i,k+j)
NEXT j
NEXT i
box=R*R
FOR m= 0 TO box
IF TOT=m THEN n(m)=n(m)+1
NEXT m
TOT=0
NEXT k
NEXT l
FOR m= 0 TO box
REM calculate Q(S,r)
n1(m)=n(m)/nr
REM calculate SQ(S,r)
IF m>0 THEN n2(m)=m*n(m)/nr
REM calculate S2Q(S,r)
IF m>0 THEN n3(m)=m^2*n(m)/nr
Z1=Z1+n2(m): Z2=Z2+n3(m)
NEXT m

lacunarity= Z2/Z1^2: PRINT “LACUNARITY”; lacunarity
```

*Box. 8.6*. Program to calculate the Fractal Dimension D of a Land mosaic. This routine has been prepared in Basic.

```
REM MS1= Number of columns
REM MS2= Number of lines
REM Patch= Value of grid cell : 0 or 1
REM NODIV= Number of divisions
REM Divider= box dimension
REM CODE= Number of boxes for each divider
PRINT "Matrix size: (x)";:INPUT MS1
PRINT "Matrix size: (Y)";:INPUT MS2
DIM patch(MS1,MS2), per(500), tboxl(500), dividerl(500), tboxll(500)
INPUT "file name"; pop$
Y=1
OPEN "I", #1, "hard disk:"+pop$
100 IF EOF(1) THEN GOTO 1000
X=X+1
INPUT #1, a
patch(Y,X)=patch(Y,X)+a
IF X=MS1 THEN Y=Y+1:X=0
GOTO 100
1000 '
PRINT "The matrix is :" :PRINT MS1, MS2
PRINT "Select the Number of dividers":INPUT NODIV
FOR M= 1 TO NODIV
PRINT "Select the size of divider": INPUT divider
divider(M)=divider
CODE(M)=MS1/divider(M)
NEXT M
FOR j= 1 TO NODIV
PRINT j, divider(j), CODE(j)
NEXT j
FOR j= 1 TO NODIV
DIM tot(CODE(j),CODE(j))
tt=0
FOR Y= 1 TO MS1
FOR X=1 TO MS2
IF patch(Y,X)><0 THEN cody=INT((Y−1+divider(j))/divider(j)):codx=INT((X-
1+divider(j))/divider(j)):'PRINT y,cody,x,codx
IF patch(Y,X)><0 THEN tot(cody,codx)= tot(cody,codx)+1
NEXT X
NEXT Y
FOR l= 1 TO CODE(j)
FOR k= 1 TO CODE(j)
CC=CC+1
IF tot(l,k)><0 THEN tt=tt+1
NEXT k
NEXT l
PRINT "cc";CC, tt
ERASE tot
```

```
tbox(j)=tbox(j)+tt
tt=0
CC=0
NEXT j

FOR j= 1 TO NODIV
PRINT j, divider(j), tbox(j)
tboxl(j)=tboxl(j)+LOG(tbox(j))
dividerl(j)=dividerl(j)+LOG(divider(j))
'Computation of regression

sumx=sumx+ tboxl(j)
sumy=sumy+dividerl(j)
sumxy=sumxy+tboxl(j)*dividerl(j)
sumxsq=sumxsq+tboxl(j)*tboxl(j)
sumysq=sumysq+dividerl(j)*dividerl(j)
NEXT j
xbar=sumx/NODIV
Ybar=sumy/NODIV


FOR l= 1 TO NODIV
diffX=diffX+(xbar-tboxl(l))*(xbar-tboxl(l))
diffY=diffY+(Ybar-dividerl(l))*(Ybar-dividerl(l))
NEXT l
sqxy=sumxy-(sumx*sumy)/NODIV

b=-(sqxy/diffY)

PRINT "FRACTAL DIMENSION"; b

END
```

*Box 8.7*. Program to calculate the fractal dimension of edges using the divider method. This routine has been prepared in Basic.

```
REM PROGRAM TO CALCULATE THE FRACTAL DIMENSION
REM REGRESSING LOG PERIMETER ON LOG AREA
REM data are from matrix produced by the routine "Clump" of MacGIS
INPUT "File name:"; pop$
INPUT "Matrix size: columns"; Ncol
INPUT "Matrix size: rows"; Nrow
INPUT "Cell length:"; length
DIM patch(Nrow,Ncol), per (500), area(500), per(500), areal(500)
y=1
```

```
OPEN "I", #1, pop$
100 IF EOF(1) THEN GOTO 1000
x=x+1
INPUT #1, a
patch(y,x)=patch(y,x)+a
IF x=40 THEN y=y+1:x=0
GOTO 100
1000'
FOR y=2 TO Nrow
FOR x=2 TO Ncol
IF patch(y,x)><0 THEN GOSUB 300
NEXT x
NEXT y
FOR y=1 TO Nrow
FOR x=1 TO Ncol
area(patch(x,y))=area(patch(x,y))+(length*length)
NEXT x
NEXT y
FOR 1= 1 TO 500
IF per(1)><0 THEN cc=cc+1
IF per(1)><0 THEN perl(cc)=perl(cc)+LOG(per(1)): areal(cc)=areal(cc)+LOG(area(1))
NEXT 1
PRINT cc
FOR 1= 1 TO cc
PRINT #2, areal(1);",";perl(1)
sumx=sumx+ areal(1)
sumy=sumy+perl(1)
sumxy=sumxy+areal(1)*perl(1)
sumxsq=sumxsq+areal(1)*area(1)
sumysq=sumysq+perl(1)*perl(1)
NEXT 1
xbar=sumx/cc
ybar=sumy/cc
FOR 1 = 1 TO cc
diffx=diffx+(xbar-areal(1))*(xbar-areal(1))
diffY=diffY+(ybar-perl(1))*(ybar-perl(1))
NEXT 1
sqxy=sumxy-(sumx*sumy)/cc

b=sqxy/diffY
PRINT "FRACTAL DIMENSION"; b
END

3000'
IF patch(x+1,y)=0 THEN per(patch(x,y))=per(patch(x,y))+length
IF patch(x-1,y)=0 THEN per(patch(x,y))=per(patch(x,y))+length
IF patch(x,y+1)=0 THEN per(patch(x,y))=per(patch(x,y))+length
IF patch(x,y-1)=0 THEN per(patch(x,y))=per(patch(x,y))+length
RETURN
```

## SUGGESTED READING

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# Glossary and Acronyms

**A/S -** Anti-Spoofing. A P-code (Precise Code) from a GPS satellite for military use that can't be received for non-military use

**Affordance** Some characters of objects perceived by organisms with a specific meaning

**Algorithm** A set of rules to produce a computation

**Almanac** Information transmitted by satellites describing the orbit of the GPS satellite

**Alpha diversity** The number of species in a collection

**Amenity** A subjective attribute of landscape based on spiritual values like peacefulness, safety, etc

**Area-sensitive species** Species sensitive to habitat size, that require large stand of the same type

**Autoecology** The ecology of a species

**Autopoietic capacity** The capacity of a system to self-organizing and to maintain a "creative" attitude across homeostatic and homeorhetic responses to changing conditions

**AVHRR** Advanced Very High Resolution Radiometer

**Bajada** A broad continuous alluvial slope extending from the base of mountain range to an inland basin in semi-arid and desert regions as in SW US

**Base station** The GPS reference station in which geographical coordinates are known with precision (see differential correction)

**Basic** Beginner's All-purpose Symbolic Instruction Code. A simple computer program language, generally used by inexperienced computer users

**Beta Diversity** The rate of change in species along a gradient from one habitat to another

**Bighorn** A wild sheep *Ovis canadensis,* living in the western North America

**Biodiversity** The number of species present in a site, the variety of living organisms

**Bio-semiotics** The branch of the semiotic that investigates the cognitive processes

**Bit map** A sequence of bits (i.e. 0/1) on the grid

**Buffer** Transitional area acting as a filter or a mitigator of disturbance processes

**Cadastral maps** Maps at scale of 1:2.000 that describe the bounds of properties, roads and hydrographic net

**Cantor dust** An infinite number of points scattered over an interval after and infinite number of operations. This is produced starting from a unit of which a generator removes at each step the open middle third

**Climax communities** More or less stable communities at the terminal stage of the ecological succession

**Cluster** A group of cells or pixels that are connected each other

**Coarse grained** When a pattern or a mosaic have large components

**Cognition** The level of knowledge of interior and exterior of every organism

**Cognitive landscape** The landscape perceived by cognitive mechanisms

**Complexity** The state of the world in which uncertainty, connection and scaling effects create self-regulating structures

**Connectedness** The physical distance from elements of the same type. Used generally to describe the distance between forest patches

**Connectivity** Functional attribute of connectedness

**Constellation** The spatial arrangement of visible GPS NAVSTAR satellites

**Contagion** A measure of the degree of clumping of land cover or vegetation types

**Contrast** (between patches) Difference in attributes of patches

**Core habitat** The central part of a habitat with very predictable (typical) conditions

**Corridor** A narrow strip of habitat surrounded by habitats of different types

**Corridor patch** A patch or a habitat that has the functions of a corridor

**Covert** Site in which three or more habitats meet

**Cultural landscape** A landscape profoundly changed by a long history of feedback between ecological processes and human activity, e.g. agriculture, forestry and pastoralism

**Data Dictionary** A description of feature and objects useful to store field survey data quickly in a GPS datalogger

**Datalogger** A hand-held, lightweight data entry computer, also used in GPS applications

**Dehesa** A belt of mosaic of pastures and scattered trees of central Spain. (See also **Montado**)

**Differential correction** Procedure to improve the accuracy of GPS data by combining data from a base station database of known coordinates and rover data collected at the same time. With this procedure the SA (Selective availability) is removed

**Discharge** (water, nutrients) The rate of discharge of water or nutrients from a porous media

**Discontinuity** The abrupt change of some characters of a system

**Dispersion** The capacity of individuals and populations to move to a new habitat or to new parts of a landscape

**DOC** Dissolved Organic Carbon

**DoD** Department of Defense. Operates the NAVSTAR satellite for GPS

**Eco-field** A spatial configuration of objects carrier of meaning for a specific living function

**Ecodiversity** The diversity of land cover type or forest type. May be used also in a cultural landscape to describe the diversity of land use and human culture integrated with ecological processes

**Ecosphere** Portions of the universe favourable for the living organisms and in which all ecological processes are contained

**Ecotone** A transition site between different habitats, a tension zone between systems of different maturities and where energy exchange and material are highest

**Ecotope** The elementary unit of a landscape, homogeneous for a particular pattern or function

**Edaphic (factor)** Physical and chemical conditions of soil

**Edge effect** The presence of higher concentrations of organisms at the edges

**Elevation mask** The angle below which a GPS receiver does not track satellites. Rover receiver generally is set to 15°

**Embodiment** A process in which the physical attributes of organism's body affects the cognitive mechanims

**Entropy** A measure of landscape disorder or unavailable energy in a thermodynamic system

**Ephemeral** A phenomenon or an organism lasting for only a short time (few days or hours)

**Evaporation** The process of transformation of liquid water in vapour

**Evapotranspiration** The loss of water for transformation in vapour by plant transpiration

**Evenness** The distribution of abundance between a collection of organisms or patches of a landscape

**File** A collection of related information stored in a computer, with a specific name

**Florida keys** Coral islets or barrier islands off the southern coast of Florida

**Fossorial behaviour** The digging or borrowing behaviour of mammals

**Fractal** An object that has fractional dimension and which at a changing scale of resolution shows self-similarity

**Fragility** An attribute of ecological systems: A system is fragile when under a perturbation regime a change of biological diversity occurs

**Fragmentation** A process by which forest cover is opened and isolated woodlots are created

**Functional heterogeneity** Heterogeneity in the spatial distribution of ecological entities (individual, populations, species, communities)

**Functional patch** A patch that has homogeneous characters for a particular function

**Fymbos** Shrub cover in South Africa (Cape Town region), similar in shape to Mediterranean maquis

**Gamma diversity** The diversity of species in different habitats along a geographical area

**Gap-phase** The process that follows the tree fall in forests and which produces clearings and regrowth by secondary succession

**Geomorphic processes** Events that modified the chemical substrate and physical appearance of facies, rocks and soils

**GIS** Geographical Information Systems

**GPS** Global Positioning System, a satellite-based positioning system.

**Grain** The resolution of an image or the minimum area perceived as distinct by an organism

**Grid map** A map in which data are stored in form of grid cell

**Guild** A group of animals with similar characters associated to functions (foraging guild, breeding guild, etc.)

**Habitat patch** A patch selected by individuals of the same species

**Hardwood forest** The wood of angiosperms trees

**HDOP** Horizontal Dilution of Precision, attribute of NAVSTAR constellation

**Home Range** The area in which a species normally live

**HRV** High Resolution Visible Scanner

**Hedgerow** A strip of shrub or trees planted in a rural landscape for signal properties or to protect crops from windstorms

**Holartic (forest)** Forest of Paleartic and Neartic zoogeographical regions (sin. northern emisphere)

**Holon** The component of the horizontal structure of a hierarchical system

**Inbreeding** Genetic exchange within related individuals

**Incorporation** The process by which a system reduces the effects of disturbance

**Individual-based landscape** The surrounding perceived by (somatic) biosensors

**Information** A basis attribute of the universe associated with order/disorder status of objects

**Information landscape** The mosaic built using the information on the surrounding perceived by individuals

**Interrefuge corridor** Strip of land that connects habitat patches considered as refuges for some species

**Interior species** Species living far from forest edges

**Isotropic** An object that is a rescaled copy of itself in all directions

**Keystone species** Species that shapes the habitat in which lives and allows the presence of other species

**Labels** The description of an object represented in a map

**Land unit** The association of ecotopes. Synonymous of microchore

**Landmarks** Objects in a landscape used by organisms for orientation

**Landscape patchiness** A land mosaic composed of many patches

**Layer** A map component of a GIS system

**Litter** Vegetation material recently fallen on the ground and only partially decomposed

**Local extinction** The disappearance of a species from a patch

**Local uniqueness** The presence of unique characters linked to a particular site

**Long-term ecological studies** Studies planned in particular sites, regions and areas in order to track ecological processes for a long period of time

**Macrochore** A region composed of an aggregation of mesochores

**Macro-scale** The level between meso- and megascale

**Matrix** The dominant component of a landscape mosaic

**Megascale** The upper level of scaling

**Mesolithic** Archeological period from about 10,000 to 4,000 years bp

**Mesochore** An aggregation of microchore

**Mesoscale** An intermediate level between micro and macro-scale

**Metapopulation** Sub-populations that are connected by movement (immigration-emigration of individuals)

**Microchore** An aggregation of ecotopes

**Micro-scale** The lower level of scaling

**Microcosm** A small world or communities compared with a larger dimension or entity

**Mistery** The possibility to gain information from the environment during an exploration

**Montado** The Portuguese part of Spanish Dehesa (See **Dehesa**)

**MSS** Multispectral Scanner, a device mounted on Landsat satellites

**Naturalness** Attribute of land meaning intactness or integrity of ecosystems

**NAVSTAR** The official name of the GPS satellites. Acronym for Navigation Satellite Time And Ranging

**Neutrality-Based Landscape** The surrounding (landscape) as perceived by a low level of bio-sensorship

**NOAA** National Oceanic and Atmospheric Administration (USA)

***Nothofagus*** Genus of evergreen or deciduous of Family *Fagaceae*

**Nutrients** (in the soil) Elements necessary for plant nutrition

**Observation scale** The spatiotemporal scale at which a process or a pattern is more easily observed (studied)

**Observed-Based Landscape** The surroundings perceived by a cultural (training) sensorship

**Outbreaks** Organism demographic explosion, generally refers to pests (mice, insect, weeds)

**Parish** A religious division of a landscape common to all western Europe. One or more villages pertain to a parish

**Pathogen** Any microorganism that produces diseases

**PDOP** Position Dilution of Precision, attribute of NAVSTAR constellation

**Pedon** The smallest unit or volume of a soil profile

**Percolation** The property of fluid to occupy a porous medium

**Percolation thresholds** The value of 0.5928, calculated on large theoretical lattices, by which a fluid percolates, moving from one side of a matrix to the other

**Perturbation** A discrete event that modifies the status of a system without catastrophic consequences. Synonymous with Disturbance

**Petrocalcic horizons** A diagnostic subsurface of soil horizon characterized by induration with calcium carbonate

**pH** The negative logarithm( $\log_{10}$) of the hydrogen-ion activity in solution

**Phreatic water** Synonymous of ground water, the water in the soil in the zone of saturation

**Physiotope** A land unit homogeneous for soil characters (see **Ecotope**)

**Phytoplankton** The plankton plants living free in water

**Pixel** Contraction of Picture Element, the smallest unit of information of a map or a raster image

**Polypedon** A group of contiguous pedons

**Prospect** An environmental condition, situation, object or arrangement conducive to the attainment of a view

**Pseudo-sink** A population with sink characters but that persists, although at a minimum level, also when the immigration of individuals from a source area is reduced

**Raster** A representation by grid cells of an object in a computer memory

**Refuge** An environmental condition, situation, object or arrangement conducive to hiding or sheltering

**Resilience** A process by which a system incorporate a disturbance by small changes in internal structure and function

**Rover** A mobile GPS receiver

**SA** Selective Availability. A deliberate error into the GPS measurements by the DoD. SA can be completely removed by using the differential correction (see **GPS** and **DoD**)

**Savanna** Tropical vegetation dominated by grasses and tall shrubs with a different density of isolated trees

**Seepage** The slow movement of water in a porous media (soil, litter)

**Self-organized** A property of a system to transform, conserve and transfer information

**Semiotic** The science that studies the way organisms translate signals received by an external world into signs used for the "private" world

**SEPM** Spatially Explicit Population Models

**Shifting-mosaic steady state** The condition in which a landscape changes in distribution of patch due to different causes, but at the end maintains the same character

**Shrub-obligate species** Species (f.i. birds) living exclusively in shrubs

**Sink** A population that becomes extinct without external immigration. May be referred also to habitats

**Sound-scape** Any sound perceived around an organism, and that in some degree creates a perceived context

**Source** A population that has a positive balance between births and deaths. May also refer to habitats

**Spacing** The ability of an organism to react to its perception of the neighboring environment

**Spatial heterogeneity** The variation across space of vegetation type or land cover

**SPOT** Satellite Pour l'Observation de la Terre, a French satellite

**Stop-over migrants** Migratory birds that spend short time in selected habitats along the migratory route to replenish energy

**Structural patch** A patch characterized by a recognizable pattern (for instance a soil type associated with a particular plant)

**Supervised classification** A method of remote sensing by which a satellite image is classified using training sets of classified patterns, land cover or vegetation

**Synecology** The study of the ecology of groups, populations and communities

**TDOP** Time Dilution of Precision, attribute of NAVSTAR constellation

**Temporal heterogeneity** The variation across time of a vegetation type or land cover

**Terraccete** A levelled piece of land on a steep slope protected downwards by a stone or mound wall

**The Everglades** The Florida marshes and wet forests subject to periodical freshwater flooding

**Thematic map** A geographical representation of a land use or vegetation cover, or other natural or socioeconomic phenomenon

**TM** Thematic Mapper, a sensor place on LANDSAT satellite

**Topology** Pattern of linkage between geographical elements

**Total human ecosystem** Conceptualization of modifications and effect of human life on the Earth

**Trampling** Soil compactation due to animal passage

**Traps** Habitats that attract species because of their favourable conditions but in which some functions such as breeding are not allowed or are suddenly interrupted by human disturbance or predation

**Tree-fall gap** Opening in forest cover due to individual tree fall

**Umwelt** The environmental surrounding as perceived by organisms

**UTM** Universal Transverse Mercatore Projection

**VDOP** Vertical Dilution of Precision, attribute of NAVSTAR constellation

**Vector** An object that has magnitude and direction

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