Landscape ecology is a discipline that studies environmental complexity, concentrating mainly on an analysis of the importance of spatial relationships between the various components (individuals, populations, communities, and land mosaics) of the real world. Defined as the spatial representation of an ecosystem, a landscape is composed of many superimposed environments as perceived by various species or modified by ecological processes such as flooding and fires. The way in which an organism perceives the environment that it inhabits is species specific, which allows us to talk of a geobotanical domain, an animal one, and an anthropic one. These complex landscapes are measured spatially by geographic information systems, and the resulting data are analyzed using a combination of geostatistics and fractal mathematics. Landscape ecology is used mainly for the management of human-scale landscapes and, more specifically, for the analysis, management, and conservation of nature; these offer the most fruitful application of the knowledge that landscape ecology provides about the workings of land mosaics.

**Introduction**

During the past few decades, it has become increasingly clear that in order to acquire a more thorough understanding of the complex processes that take place in the biosphere and, more generally, in the ecosphere, the spatial dimension of ecosystems must be broadened. An appreciation of the extent of the complexity of life on Earth has become widespread among both scientific researchers and the general public, and the globalization of environmental problems has made it necessary to broaden the scale of the analysis and of the interpretation of the phenomena involved. The broadening of the spatial scale has also led to the reassessment of the temporal one and, as a result, to the creation of a powerful and flexible analytical tool in which the spatial and temporal scales can be calibrated according to the system being considered. Ecological research, which until the beginning of the 1980s was rooted in concepts of environmental homogeneity, of equilibrium within the ecosystem, and of the separation of man from environmental processes, has undergone a profound change during the past decade. Indeed, when the spatial scale was broadened, ecological research began to view the environment as a heterogeneous system in which the variety of ecological processes are expressed as a state of dynamic equilibrium (*homeorhetic flows*) and in which the processes governed by man become an intrinsic part of environmental mechanisms. Landscape ecology studies environmental complexity, concentrating mainly on an analysis of the importance of spatial relationships between the various components of the real world.

Heterogeneity appears to be the predominant pattern in
most landscapes, and increasing importance is attached to the role that it plays in determining ecological processes. A landscape contains heterogeneous characteristics that are expressed in discrete entities known as patches, which in turn make up a mosaic that is structurally and geographically distinct. The salient characteristics of these patches, such as dimensions, shape, type of vegetation, biological richness, abundance of organisms, and flow of nutrients, contribute to the organization and maintenance of the complexity of landscapes.

Landscapes

A landscape is defined as the spatial representation of an ecosystem. Thus, rather than an entity being described entirely in terms of its function (an ecosystem), it is defined in terms of its spatial characteristics (a landscape). The concept of landscapes represents a relatively new approach and one that is also rich with significance. Indeed, as the geographic dimensions are expanded, ever more processes, together with the increased biodiversity they bring, are included. A landscape, in fact, is a system of environments, each one of which is species specific and delimited by the species. Each species recognizes the boundaries of the environment it inhabits, identifies those characteristics that favor its existence, and reacts to the environment on a species-specific scale. A landscape is therefore the sum of many species-specific systems that can be superimposed to a varying degree and that contribute to the complexity of the environment. This vision of the environment is characterized by a large quantity of information that results in a set of retroactive mechanisms that help to regulate and calibrate the various processes and that make it possible for many organisms to survive and to perform multiple roles. All this tends to promote an autopoietic capacity, or the “creative” ability of the system to adapt to new conditions through homeoretic and homeostatic mechanisms.

When studying a landscape, it is important to be able to consider the components that are of immediate interest without losing sight of the whole. Such an approach is necessarily transdisciplinary, and analyzing a landscape does much to increase our understanding of the ecological complexity of a geographic area. A landscape can vary in size from a few centimeters to tens of kilometers. In fact, the term immediately brings to mind a large area, and in almost all Western cultures it is used to denote a scenographic or geographic reality. Nevertheless, every species perceives its own particular landscape in its own species-specific way, which can even change according to the physiological context in which that organism finds itself at any moment. The landscape is therefore perceived by man as his own environment. Consequently, the study of the way in which it functions is called landscape ecology; indeed, this dimension is the nearest to the complex processes that, through his own culture, man has applied to a natural substratum.

As a result of the variety of cultural and scientific approaches, there are many definitions of a landscape as perceived by man. It is the general character of a region (Humboldt, 1807); it is a heterogeneous area composed of a cluster of interacting ecosystems that reoccur in a similar manner throughout a region (Forman and Godron, 1986); it is the sum of physical, ecological, and geographic entities that embrace and bring together all natural and human processes and their patterns (Naveh, 1987); it is a particular configuration of topography, plant cover, use of the soil, and human settlements that are delimited by natural and cultural processes as well as by anthropic activities (Green et al., 1996); and W. Haber (1996, personal communication) defines a landscape as an area of land that we perceive without paying particular attention to any one component that seems familiar to us.

Currently, most landscape ecology is concerned with landscapes that have been modified by man, even though its analytical principles and instruments can be validly applied to the study of landscapes that have not been subjected to the direct influence of man. Landscape ecology therefore studies complex systems and indeed often requires that special reference be made to a particular organism or group of organisms (Turner et al., 1995). Consequently, a landscape perceived by human beings is quite different from a landscape perceived by coleoptera (Wiens and Milne, 1989) so that when one talks of a human landscape one must necessarily consider the cultural component that is associated with it.

The Contribution of Other Disciplines to Landscape Ecology

Precisely because landscape ecology is a complex discipline, its theoretical corpus is the result of bringing together and integrating a series of approaches and applications, among which the theory of island biogeography (MacArthur and Wilson, 1967) and geographical ecology (MacArthur, 1984) occupy preeminent positions. These theories were the first to emphasize the extent to which the degree of isolation and the dimensions of an island determine species richness and abundance. Islands that are small and distant from the mainland have a smaller number of species compared to those that are larger and nearer to the mainland. Furthermore, there is an inverse correlation between the risk of extinction and the probability of colonization. The smaller the island, the greater the risk of extinction, whereas the probability that another species will colonize it is correspondingly less. This theory can also be usefully applied to so-called islands on land, environments that due to the process of fragmentation have been reduced in size and have been surrounded by other environments that are hostile for given species.
Landscapes and Heterogeneity

A landscape consists of two fundamental components: the geographic or chorological component and the topological or functional one. In fact, these two components cannot be separated without drastically reducing the amount of information that is obtained when they are considered together. By definition, landscapes are heterogeneous environments: That is, they consist of various elements that are interrelated in different ways. This heterogeneity is a very important pattern since it in fact determines the ecological diversity of any region. The heterogeneity might be expressed as physically identifiable structures, such as woods and land under cultivation, or as processes such as variations in the thermal characteristics of slopes or the degree of the environment's species-specific suitability. At any rate, the degree of heterogeneity varies according to the spatial arrangement of the single component parts. Space is therefore an important component in determining the extent of the diversity of the various forms of life. It follows that the spatial arrangement of the various entities and their processes and relevant patterns can be considered as one of the main paradigms for introducing the spatial dimension as an element that is important per se. The presentation of landscapes as components in a “nest” hierarchy (one in which the highest level contains all the other levels) that incorporates the concept of scale has been a determining factor in linking the various paradigms (Allen and Starr, 1982; O’Neill et al., 1986) and the various theories (Delcourt and Delcourt, 1988).

At the same time, a more satisfactory approach to dealing with complexity has been provided by non-Euclidean, fractal geometry (Mandelbrot, 1975), which is able to measure the complexity and the relative patterns of many natural systems and to establish relationships between elements that are only distantly connected. New theories of heterogeneity (Kolasa and Pickett, 1991) and the role of disturbance regimes in ecological processes (Pickett and White, 1985) represent significant steps forward and thoroughly incorporate the paradigm of ecotones (Hansen and Di Castro, 1992) and the processes associated with them, such as connectivity and connection (Merriam, 1984) and meta-population models (Gilpin and Hanski, 1991), into landscape ecology. The recognition of the existence of a heterogeneous structure in landscapes has also made it possible to extend and adapt Pulliam's (1988) source and sink demographic model and to redefine the roles played by single patches in a landscape.

The Study of Landscape Ecology

The complexity of the issues they deal with, together with the fact that they make reference to a range of disciplines, has led to landscapes being viewed as entities that change character according to the approach that is adopted. The main texts on landscape ecology (Forman and Godron, 1986; Naveh and Lieberman, 1994; Forman, 1995; Zonneveld, 1995) have drawn ample attention to this characteristic while nevertheless expressing very different and often divergent visions of the discipline. Indeed, whereas Naveh and Lieberman have an anthropocentric, globalizing vision, that of Zonneveld is more geographical and concerned with typological classification and the approach of Forman and Godron is more geometric and views space on a large scale as the central factor that conditions processes.

It is time to reconcile and integrate the various concepts of what a landscape is, bearing in mind the different biological components (Farina, 1998). Historically, this discipline derived from the human geographical sciences, and the first description of families of patterns and processes was strictly linked to the anthropic sphere. Recent studies, mainly in North America, on the spatial arrangements of patterns and on processes that concern the soil, vegetation, and the animal component apart from the anthropic one, have resulted in a huge leap forward. There are indeed three perspectives to be considered in landscape ecology: the human one, the geobotanical one, and the animal one.

The human perspective allows us to dismantle and reassemble a landscape according to the functional entities that are relevant to human beings. The geobotanical perspective considers the spatial distribution of biotic and abiotic components, from the landscape of the soil to that “perceived” by plants and to the distribution of vegetal entities such as woods and grassland. Where plants are concerned, “perception” is taken to mean the ability to absorb information from the surrounding environment. This is directly related to the extent of adaptation, to the rate of colonization and extinction, and to the resistance to natural and man-made stresses.

The animal perspective considers the way in which each species perceives its own environment. It is obvious that a butterfly cannot use the same environmental parameters as a deer or a fish. Its life will therefore take place in and impact a precise part of a landscape. The combination of the interactions expressed by an animal community constitutes an important conditioning factor of the landscape seen as a complex whole. Man, performing the double role of biological species and intelligent organism, should also be considered in this context.

These perspectives are not in conflict because each one of them is concerned with exploring a domain of patterns and processes that are in fact components of the entire biological and ecological system. Furthermore, there are many more points in common, such as the perception of space and the spatial arrangement of patterns and processes, than there are differences. Thus, the common strategy adopted by landscape ecologists is to insert these patterns and processes into the most suitable spatial and temporal scale.

The human dimension of a landscape is probably the most complicated in that it superimposes man's animal and cultural components. This dimension relates to processes
that have a very broad spatial and temporal scale. The biological dimension of man can be compared to that of animals, but the cultural component of humanity is unique, and it is this component that has the greatest interactive impact on a landscape, especially since man is inclined to use technologies that overcome the physical and biological limits of the natural systems in which he operates.

The three perspectives outlined previously cannot be considered separately, but their sectional nature is linked to the ability to adopt an approach that is interdisciplinary or even transdisciplinary. A landscape is so complex that even this approach does not provide explanations for all the processes; but it can shed new light on this complexity and define the limits of its own ability to provide explanations.

Landscape ecology is therefore one of the most promising ecological disciplines, and although it is highly differentiated and wide ranging, it is capable of expressing a single “spirit” linked to the finite dimension of the area of study. This discipline allows a more precise superimposition of information from the real world onto the virtual processes that today’s postindustrial culture is promoting through globalization.

Currently, there is a high risk of landscape ecology being considered entirely from the anthropocentric point of view, and this might result in its being seen as a dogmatic discipline without either theoretical foundations or experimental backing. Furthermore, it seems unacceptably reductive to consider landscape ecology simply as a form of broad-scale ecology. In fact, one of the major strengths of this discipline is its ability to transfer information through various families of processes that take place on different spatial and temporal scales and to link knowledge from precise ecological research to environmental and landscape planning activities.

Theories and Models Embraced by Landscape Ecology

The hierarchical theory and the percolation theory combine with two models of population dynamics — the meta-population model and the source and sink model — to create a powerful referential context for landscape ecology. Although they were formulated in various contexts, these theoretical elements share a common interpretation of the complexity of landscapes. They have played an undeniably important role in creating a homogeneous disciplinary corpus that offers a paradigmatic bridge over the complexities of landscapes.

The Hierarchical Theory and the Structure of Landscapes

The hierarchical theory (Allen and Starr, 1982; O’Neill et al., 1986; Allen and Hoekstra, 1992) is a useful instrument for exploring numerous patterns and processes through various scales in space and time. Considering complexity as an attribute that is intrinsic to a landscape, the hierarchy paradigm explains how the various components located on certain scales enter into contact with other ones that are visible on different scales of resolution. The hierarchical theory views a system as a component in a larger system that consists of subsystems. As one moves from one system to another, the characteristics of the phenomena change — for example, the classification of a landscape as one goes from lower to increasingly higher levels in the hierarchy: ecotope (the basic unit in a landscape consisting of biotic and abiotic elements); microchore (the spatial distribution of ecotopes); mesochore (the environmental system composed of a group of microchores); macrochore (a mosaic of landscapes); and megachore (a group of geographical elements covering several kilometers).

A watershed is an example of a hierarchical system composed of subbasins that in turn are composed of even smaller basins. A system exists independently of its components and is generally able to organize itself and to transmit information; in other words, it is able to exist as a cybernetic system. A landscape exhibits its own type of complexity, and in order to understand it fully it is necessary to focus on a certain organizational level. There are innumerable hierarchical levels and thus an equal number of systems that are nested inside them in one way or another. The behavior of a given subsystem conditions nearby systems both above and below it. The speed with which the processes unfold and thus the scale in time are specific to each level. When going from one level to another, it is therefore necessary to adjust the resolution. The hierarchical theory contributes much, for example, to an understanding of the effects of various disturbance regimes. Thus, fire is a highly destructive element for the “tree system,” but it is an element that, ecologically speaking, promotes “creativity” for the forest as a whole in that it establishes new conditions for many species of plants and animals.

The Percolation Theory

The percolation theory was formulated as a result of studies of the behavior of fluids in a medium (Stauffer, 1985) and has recently been used, with interesting results, in the creation of landscape models (Gardner et al., 1987). Unlike diffusion processes in which every particle in a liquid moves in all directions, the percolation process takes place in finite regions of the medium, which the fluid does not leave. When the fluid occupies about 0.5928% of the entire surface of the matrix, it has reached what is known as the percolation threshold (Ziff, 1986); such a state guarantees, for example, that the cells in a matrix will be in contact with each other from one side of the matrix to the other. This theoretical limit is nevertheless an important concept with regard to studying real patterns, such as the expansion of
an urban area or the spread of a wood as a result of secondary succession.

The relevance of this theory to the study of the behavior of landscapes is clear if one considers that around the critical threshold, contagion, forest fires, and demographic explosions of pathogenic agents exhibit their initial states of diffusion (Turner, 1987). Furthermore, this theory can be usefully applied to the study of animal behavior in a heterogeneous system. Indeed, the percolation process has been thoroughly tested with neutral models (i.e., square matrices with randomly filled elements). Neutral models assume a state of complete spatial independence between the various cells, and the habitats do not exhibit any autocorrelation. These models consider both the scale of resolution and the behavior of the single cells of the matrix and, for example, simulate the perception that the various species have of the environment that surrounds them. Since the perception of an environment is species specific, it is obvious that each species will perceive it as a percolating habitat (i.e., one that is more or less connected). These models can be used to predict when an environment that is in a state of fragmentation will begin to lose important characteristics, such as connectivity.

**The Metapopulation Model**

Increasing forest fragmentation is a general trend in natural environments that has created fragments of isolated woodland. For the remaining populations, fragmentation has increased the risk of extinction. It can be assumed that when a population lives in a fragmented and heterogeneous environment, it perceives the landscape in which it lives as a mosaic in which hospitable environments alternate with ones that are more or less hostile, and that contact between the various subpopulations is ensured only through processes of emigration or immigration. The risk of both local extinction and recolonization depends on the extent and existence of an exchange of individuals. The success of recolonization depends on many factors, including the ability to disperse, and these populations are therefore considered to be components of a metapopulation. The term *metapopulation* was first used by Levins (1970) to describe a population of populations (Gilpin and Hanski, 1991; Hanski and Gilpin, 1991). Metapopulations are systems in which the rates of extinction and colonization create flows of individuals that ensure a genetic connection between the subpopulations.

The metapopulation model is closely related to the theory of island biogeography (MacArthur and Wilson, 1967), but it is distinct from it in that the terrestrial systems in which the metapopulations develop are less hostile. In the theory of island biogeography, the distance between the various islands is the main barrier to dispersal, and the distance from the mainland is one of the factors that determine the rates of extinction and recolonization. In the metapopulation model, however, there is a constant relationship between the various subpopulations; as a result, the exchange of individuals and therefore of genetic inheritance is maintained at a high level. The metapopulation model can be usefully applied to fragmented areas in order to analyze their dynamics and predict the probability of extinction or recolonization of isolated populations.

**The Source and Sink Model**

The source and sink model was created by Pulliam (1988) in order to study the responses to environmental conditions among various species of birds. According to this model, which can be adapted very effectively to heterogeneous environments in which the resources are unevenly distributed, a source population is one in which the ratio between births and deaths is always above unity. In other words, in a source population there is always a surplus of individuals that will tend to leave it. On the contrary, in a sink population the ratio between births and deaths is below unity, and such a population can survive only if new arrivals from outside add to it. This model can also be used to classify patches in a heterogeneous environment according to their ability to sustain a source population or a sink population (Fig. 1). As a general rule, the larger patches in an environment will tend to act as source ones to the smaller patches. Whether a patch is a source one or a sink one will also depend on...
the seasonality of the resources and on the role that these resources play in the survival of a species at the various levels of aggregation. Indeed, this model can be usefully applied in fields outside population demography. Thus, if the resources in a given patch are such as to guarantee the survival of a species, that patch can be defined as a source patch.

There are variants of the source and sink model. For example, Watkinson and Sutherland (1995) coined the term pseudo-sink to describe an environment that appears to exhibit sink characteristics but in which, even if immigration comes to a halt, the population will stabilize at a minimum level, without disappearing. Furthermore, there are special cases in which environments with sink characteristics are so inviting to various species that they take on the appearance of source environments (Pulliam, 1996). This is the case with many environments that have been modified by man and that offer abundant resources but that do not, for example, guarantee adequate protection against predators or where, in the sensitive period for a given species, man produces a disturbance that interferes with successful reproduction or even makes it impossible. It must be pointed out that this model does not always allow one to deduce the qualities of an environment, especially if the demographic criterion is applied. There are times when a sink environment can be inhabited by more individuals than a source one, and there are populations in which most of the individuals inhabit sink patches.

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**Ecotones**

The heterogeneous nature of landscapes ensures that there is contact between patches with varying characteristics (Pickett and White, 1985; Hansen et al., 1992). These junction zones are called ecotones. Clements (1905) described ecotones as zones of tension in which the species of neighboring communities meet. Clements was the first to use the term, which is based on the two Greek words, *οίκος* and *τόιος*.

Ecotones can be defined in many different ways, according to whether one is considering patterns, processes, or fully fledged habitats. They are therefore also habitats that serve as meeting points for species that are able to fully exploit the frontier zone characteristics of these environments (Ricklefs, 1973). In fact, even though the concept of ecotones is simple, their scalar characteristics complicate the task of studying them. For example, the closer one gets to an ecotone, the more difficult it becomes to distinguish what was clearly visible from a distance. Furthermore, the study of ecotones is complicated not only by these scalar characteristics but also by the fact that every biological species perceives and interacts with the environment in a species-specific way, with the result that the position of ecotones varies from species to species (Fig. 2). Thus, ecotones that can be identified by analyzing an aerial photograph or a geological map do not always exist as far as every species is concerned.

Ecotones are important structures with regard to the functioning of landscapes. Indeed, an exchange of nutrients, water, spores, seeds, and animals takes place within these juncture zones between different patches. The fact that they are transitional zones also makes them excellent indicators of climatic changes linked to the increase in CO2 and atmospheric pollution. Ecotones also have high rates of primary and secondary productivity since they generally benefit from the various characteristics of their constituent environments. In environments that have been modified by man, ecotones that are composed of copses, hedgerows, rows of trees, and the edges of fields are often refuge areas for many species that are sensitive to the disturbance regime created by man.

Along rivers and in lagoon areas, ecotones are junction zones between terrestrial and aquatic environments, intercepting the flow of nutrients moving from one to the other. The importance of ecotones has been recognized for a long time (Clements, 1897; Livingston, 1903; Griggs, 1914). Although authoritative ecologists have emphasized their importance at various times (Weaver and Clements, 1929; Odum, 1959; Daubenmire, 1968; Ricklefs, 1973), only recently have systematic studies on the subject been carried out (Di Castri et al., 1988; Naiman and Decamps, 1990; Holland et al., 1991; Hansen and Di Castri, 1992; Risser, 1995).

It now seems that the study of landscapes with reference to ecotones is capable of shedding much light on the way in which matter, energy, and individual organisms interact with a heterogeneous environment and thus with the very complexity of landscapes. It is no coincidence that the edges of mosaics have a great influence on the richness and the move-
ment of organisms, on the flow and accumulation of matter and energy, and on the spread of disturbances. In order to understand ecological processes, it is therefore essential to study ecotones, especially when the object of study is landscapes, which by definition are a part of the real world that we have an interest in investigating. Ecosystem ecology, which focuses mainly on the mechanisms that operate within an ecosystem and which analyzes the internal parts of homogeneous areas, differs considerably from landscape ecology, which is concerned with the functioning of ecological systems operating within a geographical context.

It is possible to classify ecotones according to their origins. Holland (1988) suggested four types: ecotones that are created and maintained through human disturbance (hedgerows, plow land, and hay fields); those that are created and maintained by natural processes, such as ecological succession or the bridge between terrestrial and aquatic environments that results from beavers’ dams; those that are created by natural processes and maintained by man, such as coastal lagoons or riparian woodland; and those created by man and maintained by natural processes, such as the marshy areas around artificial water reserves.

Generally, there are substantial differences between natural and man-made ecotones. In the former, the transition from one patch to another is gradual, whereas in the latter it is sudden and clearly defined.

**Characteristics of Ecotones**

Although not easy, it is nevertheless possible to identify the structure and functions of an ecotone. An ecotone covers the whole junction zone between one system and another. Its shape can be linear, as in man-made ecotones, circular, or convoluted, and it will determine the rate of transfer of environmental information, energy, and matter through the ecotone.

The biological structure is determined by the biomass or density of the dominant organisms. The structural contrast is determined by the difference between the structure of the ecotone and that of the neighboring environments. The internal heterogeneity is determined by the variability of the changes within the ecotone. The density of the ecotone is determined by the ecotonal surface area of a given area. There are also other important functional variables such as stability, which is a measure of the degree of the ecotone’s susceptibility to change. Resilience, on the other hand, is a measure of the ecotone’s ability to return to its previous state following a disturbance.

Both internal and external factors condition the organization of ecotones. The external factors are determined by processes that act on landscapes, and the internal factors represent elements of discontinuity. Many animal species, for example, create conditions that are hostile for others; furthermore, on an intraspecific level, territoriality can display ecotonal characteristics that are similar to a change in the vegetational conditions within a mosaic. Some species of plants modify the pH balance of the soil to such an extent that they create ecotonal conditions that are more or less hostile for other plants. The shade produced by a canopy can reduce the ability of other plants to grow. Many invasive species, such as the Jerusalem artichoke (*Helianthus tuberosus*), grow so densely that they prevent other species from establishing themselves.

Many animal species create ecotones as a result of their activities. An example is a small mountain field mouse, *Microtus nivalis*, that lives in grasslands above the treeline. Its incessant search for food, which does not even stop in winter, has a major impact on the distribution of the bilberry (various species of *Vaccinium*), whose evergreen stems it eats, especially in the cold season (Farina et al., 1986). Similarly, as a result of digging holes and making molehills and nests above ground level, moles, ants, and termites modify the plant cover and even change the microtopography of the soil.

In summary, ecotones can be found both on a mega-scale, such as a bioclimatic region, and on a microscale, such as an area covering just a few square centimeters of ground. The role that they play in a landscape is fairly clear. They represent semipermeable membranes that allow processes of passive diffusion, such as the movement of air or water masses carrying matter or organisms, and also processes of active diffusion, by which organisms move biomass from one part of a landscape to another, thus modifying the environmental information as well.

There is no doubt that the presence of ecotones contributes to the stability of a system by guaranteeing a complexity that reduces the risk of sudden deterioration and the loss of the system’s autopoietic capacity. Thus, a riparian ecotone (consisting of the vegetation along the bank of a river) reduces the effects of flooding by retaining, among other things, large quantities of organic substances that are then used in the food chain. Many organisms, including most amphibians, live only in ecotonal zones. The considerable species richness of the coral reefs, for example, is a function of the ecotonal characteristics of these structures. Furthermore, the greatest concentrations of plankton species are to be found in areas in which large masses of seawater meet.

Animal richness and abundance are greater along ecotones than in neighboring areas, but the linear nature of these environments also increases the risk of predation. In other words, these structures can play a variety of roles, even if by themselves they do not represent paradigms that are fully able to explain the complexity of landscapes or, therefore, the way in which they function. However, if this paradigm is coupled, for example, with the source and sink model or with the hierarchical theory, the combination is capable of yielding a great deal of information.
Cultural Landscapes

Most terrestrial landscapes have been profoundly modified by man, who has built towns, cut down forests, changed the vegetation, constructed roads and motorways, and brought about changes in the climate. In terms of the perspective adopted by landscape ecology, these modifications affect the spatial arrangement of patches, modify the fragmentation of large forest patches, and increase the number of transitional zones or ecotones.

Such modified systems exhibit an increase in both the fragmentation of the original forests and environmental heterogeneity. In these cases, landscape ecology is a discipline that offers an increasingly useful analytical tool in that it allows ecologists to study patterns and processes on different scales, including environments that have been modified by man (Fig. 3). Therefore, this approach has an increasingly important role to play in many forms of human activity that are directly related to the environment and its characteristics. Indeed, landscape ecology is able to study ecological processes over a broad range of spatial and temporal scales that reflect the complexity of the systems. By applying this discipline, it is possible to manage key species, residual forest zones, and edge networks and to influence or decide on urban development policies. Specifically, it can be applied to the problems of many landscapes that, having been modified by man, have acquired a high value in terms of complexity, biodiversity, and scenic beauty. These systems are called cultural landscapes; that is, landscapes that have been subjected to a man-made disturbance regime for a long time and in which the character and spatial arrangements of the patches are the result of complex retroactions between man and nature.

Cultural landscapes reflect the interactions between man and the natural environment and are complex phenomena with identities that are both tangible and intangible (Plackter and Rossler, 1995). In 1991, the secretary of the United Nations Educational, Scientific, and Cultural Organization set out a series of guidelines for identifying these landscapes. They generally exhibit a complex structure consisting of a fine-grained mosaic in which the physiotopes, or physical units of the landscape, are markedly localized and are used for specific and appropriate purposes (e.g., agriculture, forestry, and grazing). In upland and mountain areas, the slopes have often been terraced in order to facilitate the working of the land and, at the same time, to reduce erosion and retain nutrients (Fig. 4).

Cultural landscapes might represent a useful model for testing ways of ensuring that man’s presence does not destroy resources or cause irreversible disruption to the environment. Currently, such an aim might seem utopian, granted the universal presence of technology, but the lesson that cultural landscapes teach us cannot be ignored and...
Ecosystem management can take place on at least four organizational levels. Each level requires instruments that are attuned to a particular spatial and temporal context.

**FIGURE 5**

Ecosystem management can take place on at least four organizational levels. Each level requires instruments that are attuned to a particular spatial and temporal context.
Principles for the Conservation of Nature Reserves

Various principles deriving both from the theory of island biogeography (MacArthur and Wilson, 1967) and from the combination of paradigms in landscape ecology allow us to outline procedures for the conservation of areas of interest. First, it is important to estimate the minimum surface area involved. A tropical forest, for example, must be large enough to allow biodiversity. In temperate environments, even forests of a modest size support a high degree of biodiversity. Contiguous areas conserve more inner-forest species than disjointed ones, even when the total surface area is the same. In forest environments, patches that are separate but nevertheless near to each other have a greater number of species than patches that are far apart; also, patches that are disjointed but linked by corridors of protected areas are more conducive to biodiversity than patches that are completely isolated.

Granted similar environmental values, circular protected areas are preferable to elongated ones since the latter have a higher ratio between the perimeter and the surface area. These principles draw attention to the importance of surface area, the shapes of the patches, and the connection and the development of the ecotones.

Disturbance Regimes and Conservation

Increasingly, knowledge of the patterns of land mosaics appears to be an important element in the conservation of nature. In particular, large-scale disturbance regimes play a fundamental role in maintaining ecological processes (Baker, 1992). It is clear that disturbance regimes need to take place within large areas so as to affect only a part of the system. Indeed, in the case of fires, it is important that many patches should survive so as to create a shifting mosaic and enable disturbed patches to recover via secondary succession. Climax communities can thus be conserved if they are surrounded by a buffer of younger successional communities.

It is nevertheless unrealistic to hope that large areas will remain undisturbed by human activity, and thus the role of landscape ecology is to study a whole range of variables in order to evaluate the ability of different mosaics — forest remnants, land under cultivation, river systems, and urban areas and infrastructures — to support a reasonable degree of biodiversity. One of the main rules in delimiting a protected area is to ensure that it will include a zone of a certain minimum size in which disturbance dynamics can operate. In other words, the area should contain groups of patches that are subjected to a disturbance regime and that will ensure that the system is relatively stable in the short term. This should result in the creation of a shifting mosaic that has the greatest chance of guaranteeing ecological complexity. The boundaries of a nature reserve should coincide with the outer limits of disturbances, such as the line beyond which floods do not extend or at which fires burn themselves out naturally. It is advisable to avoid identifying a nature reserve with just one type of habitat; furthermore, it is desirable, where possible, to impose certain restrictions on activities beyond the boundaries of the reserve (Halladay and Gilmour, 1995) so as to enable the various processes and species to perform their functions fully.

Corridors and Conservation

Corridors, or narrow strips of a given environment that are wedged in between different environments, are very popular among planners but give rise to some perplexity among ecologists (Harrison, 1992). As often happens in a complex system, the function of a corridor does not always coincide with patterns such as hedgerows, rows of trees, and watercourses. In some cases, these structures are genuine corridors, but in others they do not function as corridors even though they exhibit patterns associated with them.

The more mobile species tend to move along preferential routes, but it is not always possible to identify these by applying human-scale criteria. Morphological structures such as canyons and mountain ridges often attract animals, for example, because they are easy to travel along. Hares tend to move along tracks made by domesticated animals, and the same is true of wolves and many other small mammals. Certain large carnivores, such as pumas, do not expect to find much prey in corridors, and therefore they move along them relatively quickly. For many animals, knowing their territory is essential for survival. This is true both of herbivores that move from one grazing site to another and of predators that systematically hunt for their prey in their territory.

The Conservation of Habitat Fragments and Relict Populations

In environments that are dominated by man, it is very common to find fragmented zones inhabited by more or less isolated populations whose survival depends on the degree of connectivity between the patches (Fig. 6). At the local level, populations can die out in certain patches; however, provided that this does not happen at the same time in all of them, the species is guaranteed to survive at the mosaic level. The size, shape, and quality of patches have a major influence on reproduction and the risk of predation. The qualitative character of a patch is not just a function of its shape; indeed, two patches of similar size but with different shapes have notably diverse ratios between surface area and volume.

Ecological Conservation and the Conservation of Processes

When using the paradigms of landscape ecology, it is easier and more realistic to pursue conservation policies directed at flows and processes rather than to concentrate on
the conservation of a given species, at least when there are no particularly important species to conserve. It often happens that a species is present for short periods ranging from a few days to a few years; in this case, it will often be associated with particular stages of ecological succession. Furthermore, the rarity of a species is often a function of its demographic cycles, and it is possible for a species to be rare on the margins of its habitat and very common in the center. For example, the conservation of the migratory flows of birds from the western Palearctic cannot involve protecting just one single species but must involve identifying the areas in which the birds stop during migration. Most land migratory birds stop in environments other than those in which they winter and reproduce, and, as with warblers and thrushes, like open areas such as grassland or shrub-rich savanna, both of which offer ample opportunities for feeding. On the contrary, some birds are specialized during reproduction but become generalists during migration.

Hierarchical Patterns within Landscapes and the Conservation of Biodiversity

When a landscape is viewed as a hierarchical system, its various components exhibit a range of dynamics that vary according to the closeness of the relationship. It is therefore impossible to conserve these systems without taking this consideration into account, and in doing so one tends to conserve all elements of the biodiversity contained within a landscape. Once the widely held misconception concerning species conservation are cast aside, the conservation of both biological and ecological diversity becomes a strategic objective. Granted that this does in fact occur, modern economic models can coexist with biodiversity in such a way as to guarantee solutions that are ecologically valid. In other words, in a world that is dominated by man, it is essential to find disturbance regimes that mimic the natural disturbances that trigger environmental dynamics and that also promote a satisfactory level of economic activity. Indeed, the socioeconomic crises that have affected various societies at different periods in history and in different parts of the earth have generally been provoked by the sudden desynchronization of ecological and socioeconomic processes.

Methodological Approaches to Studying Landscapes

The spatial processing of data is a vital aspect of landscape ecology and requires a series of instruments, some highly sophisticated, that are able to collect and process geographical and ecological information. The instruments and techniques range from remote sensing to geographic information systems (GISs).

Analysis is carried out on at least two main levels. The first is concerned with the shape and size of the patches that make up a landscape, whereas the second is concerned with the characteristics of the land mosaic (Fig. 7). Consequently, it is important to consider the ratio between the length of the perimeter and the surface area of patches as well as their shape and size. An analysis of a land mosaic must first involve measuring the diversity between patches as well as their nearness and the extent of their aggregation. The distances separating the patches are particularly important with regard to estimating the degree of connectivity that any one system is able to guarantee for a given organism. Furthermore, greater distance necessarily implies an increase

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in the risk of predation and a reduction in the likelihood of vector transport (the transport of matter or energy through the agency of physical forces of the movement of animals). Some techniques are based on an analysis of electronic images and are a function of the characteristics of single pixels. Such analyses can be carried out using data that are expressed in raster format (in which a process is represented by cells, pixels, or discrete spatial units).

The concept of lacunarity in a fractal distribution (Mandelbrot, 1975) provides the basis for an interesting approach to studying spatial patterns. An object with low lacunarity does not change when it is moved, whereas one whose gap distribution has a high degree of heterogeneity takes on a different spatial configuration when it is moved (Farina, 1998). It therefore seems useful to study environmental heterogeneity in terms of lacunarity. Since the analysis of edges is particularly important in this context, the complexity of a landscape can be studied not only with reference to the heterogeneity of the patches but also with reference to that of the edges (Fig. 8).

**Fractal Patterns in Landscapes**

The spatial distribution of organisms and their aggregation reflects the heterogeneity of landscapes. Indeed, the distribution of organisms is determined by the unevenness of the distribution of resources and, therefore, of biomasses. Fractal geometry (Mandelbrot, 1975) offers a new and promising way of measuring this complexity.

In environments that have been modified by man, regular geometric or linear shapes predominate. In a natural system, however, the irregularity of the shapes precludes an Euclidean approach, which is unsuitable for describing environmental complexity. Fractal geometry is considered to have many promising applications, including the analysis not only of patterns but also of phenomena such as the unevenness of the distribution of organisms, their movements, and, more generally, their behavior.

The term *fractal* was coined by Mandelbrot in 1975 to refer to an irregular object whose irregularities are exhibited on every scale. A fractal can be taken to mean an object or a pattern with a highly convoluted character. When a fractal object exhibits broad-scale patterns that repeat on smaller scales, such an object is said to demonstrate self-similarity.

There are two different types of fractals: regular ones and random ones. With the former, the self-similarity is the same on every level; in other words, the object is a copy of itself on every scale. The latter category, on the other hand, includes natural fractals such as clouds, coastlines, and organism abundance. However, self-similarity that is identifiable only statistically is a scale-dependent concept. For example, coasts are fractal objects, and their length depends on the scale of resolution that is used. Fractal geometry has a broad range of applications that include such areas of the natural sciences as geology, hydraulics, soil texture, dynamics, microbe transport, and plant structure. Fractal analytical techniques are particularly useful for studying objects which, due to their scalar properties, exhibit special complications. Thus, the abundance of an organism is a function of the scale with which environmental information is aggregated—that is, the degree of resolution that is used.

**Geographical Information Systems**

A GIS uses technology with which it is possible to process spatial data with computers and data input instruments such as digitizers and scanners and then express these data in graph form with printers and plotters. A good GIS generally makes use of digital cartography, remote sensing, and database management (Burrough, 1986).

GISs are considered indispensable for analyzing phenomena such as vegetation patterns, the distribution and movement of animals in a landscape, changes in the use of
soil, and the modeling of ecological processes (Tomlin, 1990; Coulsun et al., 1991; Maguire et al., 1991). There are two types of GISs: vectorial ones and raster ones. The former give a more accurate image of objects that reflects their natural contours, whereas the latter breaks the object into discrete parts or cells (pixels). The advantage of the raster system is mainly the ease with which information can be handled. Indeed, groups of cells that form part of a matrix can be aggregated, compared with their neighbors, and then reaggregated for different degrees of resolution. Furthermore, information from satellite images is in raster format and is relatively easy to handle with a raster GIS. The disadvantage of this system, however, is that it uses a great deal of memory space to store information.

Remote Sensing

The patterns in a landscape are generally easy to identify on satellite images, especially when \( 10 \times 10 \)-m sensors are used. The degree of resolution that is available for analyzing large geographical areas varies from 10 to 30 m per pixel and is sufficient to provide information on the patterns of the landscape under observation. It is indeed possible to gather a great deal of information from large areas, and remote sensing techniques can highlight transition zones between various environments. The complexity of the edges is a good indicator of the processes taking place in a given area. Remote sensing techniques make it possible to locate the position on the ground of patterns identified by sensors mounted on satellites. These global positioning systems (GPSs), which were developed for military purposes and for air and sea navigation, are now available at an affordable price (Leick, 1990; Hofmann-Wellenhof et al., 1993) and offer great potential for application in the field of ecology (Trimble Navigation, 1994). Using triangulation, a group of satellites are able to identify the rover’s whereabouts on the ground with a degree of accuracy ranging from 25 m to a few centimeters, depending on the configuration of the hardware. Thus, it is possible, due to GPSs, to designate areas, locate animals, and track their movements. Similarly, it is possible to scan an environment and take a census of birds by locating the sightings (Farina, 1998). The information is stored in real –time, and then at the end of the work session it is transferred to a GIS for processing. This technique makes it possible to carry out ground-level observation of patterns such as watercourses, coastlines, or ecotones.

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