## Perspective

# The eco-field hypothesis: toward a cognitive landscape

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#### Abstract

Cognition is recognized as an essential component of the living strategies of organisms and the use of cognitive approaches based on an organismic-centered-view is discussed as a strategy to aid the advancement of landscape ecology to a more independent scientific discipline. The incorporation of the theory of information, the theory of meaning and the Umwelt, and the biosemiotic models into the landscape ecology framework is described as the necessary step to create a common paradigmatic background and operational tools to develop basis for a cognitive landscape ecology. Three cognitive landscapes (neutrality-based landscape, individual-based landscape and observer-based landscape) have been described as the result of distinctive mechanisms to extract information from a cognitive matrix based on a growing literature of (bio)semiotic exchange. The eco-field hypothesis is presented as a new possibility to describe landscape processes according to an organismic-centered-view. The eco-field is defined as a spatial configuration carrier of a specific meaning perceived when a specific living function is activated. A species-specific cognitive landscape is composed of all the spatial configurations involved for all the living functions for a particular organism. Eco-field hypothesis offers a detailed vision of (habitat) environmental requirements and creates a novel conceptual bridge between niche, habitat, Umwelt and the methodological approaches of spatial ecology. Finally the eco-field hypothesis promises a new testing ground for experimental investigations in landscape ecology and in related disciplines including environmental psychology, cognitive ethology, cultural ecology, landscape aesthetics, design and planning.

## Introduction

In the recent time, the landscape has been defined by ecologists in different ways according to the epistemological approach based on a geographical heterogeneous entity, or a chorological entity, or a holistic entity, which the human mind enters as major component (Naveh and Lieberman 1984; Forman and Godron 1986; Nassauer 1995; Pickett and Cadenasso 1995; Zonneveld 1995; Naveh 2000). Some definitions have emerged from a dynamic view of the landscape (Antrop 1998) in which processes and patterns in turn influence individual, populations, communities and resources (Turner 1989; Risser 1989; Milne 1992; O'Neill 1999; Turner et al. 2001). In some cases, the landscape is not considered *per se* an entity, but as a conceptual framework (Appleton 1975; Gibson 1979; Bourassa 1991), or a functional ecological space (f.i. Risser et al. 1984; Wiens et al.

1993; Hobbs 1997) in which to study particular processes, important at the interface between human-regulated systems and natural processes. The landscape can be regarded as a domain, or a scaled space in which to investigate and address a wide spectra of ecological processes (Bastian 2001). This vision is strongly culturally oriented and, for instance, the major differences between the European and American landscape ecology school arise definitively from this vision (Farina 1993; Naveh 1995), with the European school based more on a cultural orientation and the American school on a bio-centric orientation.

Moreover, great attention has been focused by ecologists on emerging properties of the landscape including connectivity, fragmentation, presence of edges and corridors (f.i. Wiens 1995; Danielson and Hubbard 2000; Nicholls et al. 2001; Mabry and Barrett 2002; Baudry et al. 2003; Jordan et al. 2003), linking population ecology (With and Crist 1995; Hanski 1999; Goodwin 2003) and ecological processes (Miller and Urban 2000).

If we accept that the landscape is a functional space in which ecological processes are in action, we can further define the landscape in three ways: as a domain, as a system and finally as a unit (Farina et al. 2005). This statement is in line with the theory of complexity (f.i. Merry 1995), that foresees several possibilities to distinguish the landscape and emphasizes the role of the observer (f.i. Wu and Marceau 2002).

It follows that landscape ecology can be valued as an integrated ecological science (sensu Odum 1977), since it has the great merit to have introduced the geographical dimension into ecological studies, therefore bridging human and natural sciences (Tress et al. 2001). Landscape ecology has significantly contributed to develop planning procedures as well as nature conservation and management policies (f.i. Bissonette 1997; Gutzwiller 2002; Liu and Taylor 2002; Bissonette and Storch 2003; Forman et al. 2003). The idea that resources and processes have an heterogeneous spatial distribution, has accelerated, on one hand the sunset of the ecosystem paradigm (O'Neill 2001), but at the same time has offered a new perspective, which challenges toward the foundation of a science of landscape.

Some authors (f.i. Hobbs 1994) have argued that landscape ecology is a science searching

for an identity. We agree with this vision, landscape ecology is very young science and needs to grow and to self-reinforce, adopting a more robust theoretical background (Wu and Hobbs 2002).

From these premises the goal of our contribution is to present an alternative way to study the landscape, different from an ecosystemic perspective (*sensu* Golley 1993) and based on an organismic-centered-view. This approach requires new epistemological support from biosemiotics and cognitive sciences (f.i. environmental psychology, cultural ecology, etc.), and offers the potential for novel experimental settings to carry out investigations on the relationships between patterns and processes, which will be more difficult to perform than "traditional" landscape ecology research approaches (Wiens 1992).

# The organismic-centered-view of the landscape (ecology)

One of the most popular definitions of the landscape is the vision that people acquire by looking around. This definition seems, at a first sight, too trivial and oversimplified, but it is simple and immediate. When the landscape is not simply considered a fixed and structured entity, and perceived in the same way by every organism, but rather as a context for an organismic-centeredview, new paradigms to guide and to support this reasoning are required. The island biogeography theory (MacArthur and Wilson 1967), percolation theory (Stauffer 1985; Ziff 1986), neutral models (Gardner and O'Neill 1991) and metapopulation models (Hanski and Gilpin 1997), are some of the theoretical frameworks that have been used for generating hypotheses during the "infancy" of landscape ecology. Likewise, theories like information theory, theory of meaning and biosemiotics must be considered to develop additional paradigms capable to advance the landscape ecology from an ecological discipline to a "science of landscape". We are aware, of course, that we are just at the beginning of the process, convinced that several other perspectives like the cognitive sciences (f.i. Ulrich 1983; Bourassa 1990, 1991) have to be considered and incorporated into landscape ecology for it to become a true science of the landscape.

#### Information theory and landscape

Information has been defined by Stonier (1990, 1996) as a fundamental (physical) property of the universe and not simply a product of the human mind. Information reflects the level of organization of every living and not living system, and it is inversely correlated to thermodynamic probability. Information exists either as a structural information, as kinetic information, and in a form where information and energy are interconvertible.

To complete this argument we have also to add to the (physical) information the organic information as an objective-but-non-measurable entity, and definitively a "nominable" entity (Barbieri 2003a).

In order to transfer information from one system to another we need mechanisms that recognize and decode information. The theory of meaning and biosemiotics approach can each provide paradigmatic and modeling tools link information of systems with those of organisms (Cropley 1998a, b).

#### The theory of the meaning and the Umwelt

According to Jacob von Uexküll (1934, 1940), every organism has a specific vision of the surroundings, the Umwelt. Such a subjective world or a species-specific model (sensu Sebeok 1995), is composed of "perceptual" and "effector" components (see also Deely 2001). This vision, known also as "the theory of meaning", completely reverses the habitat concept and creates the premises for a more functional and organismic view of the world (Bateson 1973; Sharov 1998). Every signal that is operationally transformed into a sign with a specific meaning, is considered a receptor cue according to this perspective. Searching images and familiar paths are two close components of the operational space in which the Umwelt is active. The behavior of the tick (Ixodes ricinus), a common skin parasite of mammals, has been used by von Uexküll (1934) as an example of the Umwelt model. After mating, the female tick climbs onto vegetation (bush or tree) and remains waiting for a specific cue: the odor of butyric acid, a substance emanated by the skin glands of all mammals. This acid acts as a signal for the tick to move

downward. If the tick is lucky, she lands on a mammal's hair, and attracted by the mammalian warmth, immediately burrows into the skin to pump its blood. The Umwelt of the tick is quite simple and is composed of three "perceptual" cues (smelling of butyric acid, mechanical stimulus of hair and temperature stimulus from the mammalian skin) and three effectors cues that allow the tick to jump on the mammal hair, to search for the warm skin and to burrow to suck blood. In the modern cognitive sciences the Umwelt concept can be found with a different vocabulary in the "affordance" hypothesis (Gibson 1979; Hirose 2002). This theory of meaning allows one to assign values to every object from an organismic perspective. It is although popular theory among semioticians (Sebeok and Umiker-Sebeok 1991; Sebeok 1995), only recently it has been seriously considered by biologists (Barbieri 2001; Nöth 2005).

This theory of meaning is in contrast with the "traditional" vision of the landscape as a geographical matrix or mosaic, common to every organism. The organismic-centered-view is simply the vision that every living being has of its surrounding world. The projection of such an organismic-centered vision into a neutral matrix, has been one of the major causes of epistemological confusion among several disciplines related to the landscape including geography, landscape architecture, ecology, biosemiotics, animal behavior, and anthropology (see f.i. Ingold 2000: 190–193).

#### **Biosemiotics**

Recently, Kull (1998a, b, 2005) has emphasized the role of biosemiotics, as an emerging branch of semiotics, defined as 'the science of signs in living systems'. Biosemiotics investigates the biological basis of semiosis from molecular to cell biology (semantic biology: *sensu* Barbieri 2003b), and from animals (zoosemiosis: Sebeok 1972) to plants (phytosemiosis: Nöth 2005). For instance, the biosemiotics approach to bird acoustic communication consists in the study of the sound patterns structured into so-called syllabes, phrases, verses and strophes, and the combination of these elements. Such sign repertoires are analyzed in terms of a structural language used by an individual to manifest itself and to communicate cognitive

status to other individuals (see f.i. Gil and Gahr 2002). The combination of such signs contributes to the creation of an acoustic landscape in which animal repertoire and environmental noise are closely and explicitly related (f.i. Brumm and Todt 2002).

Biosemiotic mechanisms by which an organism interacts with its surrounding are used not only by animals but also by plants (see f.i. Krampen 1992; Kull 2000; Dicke and Bruin 2001). Plants do not have a nervous system but employ meaning-factors of their dwelling-integument (von Uexküll (1934) 1992: 33) to perceive the external world (Several examples of phytosemiotics can be found into the literature, f.i. the intraspecific transfer of signals in Alnus glutinosa (Tscharntke et al. 2001), the symbiotic or parasitic relationships (e.g. between Cuscuta and Urtica), between plants and fungi (mycorrhyza), between plants and bacteria (e.g. Trifolium and Rhizobium) and the mimicry interactions between plants and insects (see f.i. Wickler 1971).

#### Mechanisms for a cognitive landscape

After the presentation of the theory of information, the theory of the meaning (the Umwelt) and biosemiotics, we are ready to introduce the 'cognitive landscape' hypothesis as a new epistemological approach to investigate and interpret the complexity of the landscape around us. Cognition in ecology is not a novelty (Real 1993; Lima and Zollner 1996: Dukas 1998), although some difficulties to introduce such vision into the ecological realm remain (Bennett 1996; Healy and Braithwaite 2000). Cognitive phenomena have been considered with hostility by ecologists, but today modern cognitive ethology is validating the importance of mental representation (Beer 1996; Beugnon et al. 1996; Benhamou and Pouchet 1996; Shettleworth 2001; Bingman and Able 2002) although epistemological and communication gaps persist. For instance many insects utilize cognition to represent spatial and temporal information. Reinhard et al. (2004) have demonstrated that honeybee (Apis mellifera), in addition to the dance language, utilizes a scent-triggered spatial memory to locate food sources. Bees, trained to forage in two distinct localities associated with specific (rose and

lemon) scent, were able to visit the experimental feeders after the injection of rose and lemon scent into the hive. This experiment suggests that each injected scent triggers visual memories of a specific location that the trained bees had previously visited. Further evidences of the spatial cognition hypothesis are presented by Ward and Saltz (1994). These authors observed that dorcas gazelles (*Gazella dorcas*) sample their environment during foraging traits moving along a search path that deviated considerably from a random walk.

Edwards et al. (1996) have experimentally confirmed the ability of sheep to use spatial memory to locate preferred food patches, and to associate different cues with different rewards. Familiarization with the area around the natal territory has been argued by Matthysen (2002) to explain the sedentariety of blue tit (*Parus caeruleus*) populations.

The starting point of our reasoning is based on an hypothetical 'cognitive matrix' in which information (*sensu* Stonier 1990, 1996) is under a 'compressed' status. This means that a plurality of mechanisms has created the conditions for an informative world in which structures and energy are abundant and distributed in a stochastic fashion. Every living organism interacts with such 'cognitive matrix' extracting the information that form the basis of three specific cognitive landscapes: the neutrality-based landscape, the individual-based landscape and the observer-based landscape (*sensu* Farina et al. 2005) (Figure 1).



*Figure 1.* The three 'cognitive landscapes' perceived by organisms when information is extracted from a compressed cognitive matrix. The neutrality-based landscape is composed by information not converted into a specific meaning. The individual-based landscape is created by the distinct perception of surrounding objects by specific bio-sensors. The observer-based landscape emerges when cognitive 'sensors' are used.

The neutrality-based landscape is a context from which no specific carriers of meaning are extracted. This neutrality-based landscape represents the surrounding context perceived without the assignation of any explicit meaning.

The individual-based landscape is the result of 'de-compressed' information extracted by bio-sensors and specifically related to objects as carriers of meaning.

Finally, the observer-based landscape is the result of the way to extract information by using mechanisms stored in a non genetic memory. This last procedure uses at least three different mechanisms (f.i. learning by trial-and-error mechanisms, use of social cues from a 'public information' *sensu* Danchin et al. (2004), and cultural layouts (f.i. Bourassa 1990) to extract further information and to create a perceived landscape.

The neutrality-based landscape can be regarded as the result of a primitive mechanism to obtain information. The further step is initially represented by a biosemiotic process that assigns a meaning to the extracted objects and produces the individual-based landscape, followed by a cognitive process of interpretation that creates an observer-based landscape. We could represent these steps, from neutrality-based landscape to observer-based landscape, according to a level of growing (bio)semiosis between organisms and their surroundings.

The hypothesis of three 'cognitive' landscapes can be easily allied with other hypotheses of landscape perception. For instance, the prospectrefuge theory (Appleton 1975: 73), by which environment affords a certain amount of prospect (open view) and refuge (concealment, protection), can be incorporated into the mechanisms that produce the observer-based landscape hypothesis.

Petherick (2000/01) studying the effects of the environmental design on human fear of crime at a Canadian university campus, has demonstrated a difference in safety perception between female (more sensible to environmental design) and male student populations. The different 'personal geography' of women and men has been explained in terms of cultural conditioning. The spatiality of women's fear has been argued in terms of the inequality of women inside the society that creates a sense of powerlessness.

This last example can be revisited in term of landscape perception. Petherick found that female

students do not pay attention to campus when they cross the field waiting for a class lesson in the early morning. They perceive a neutrality-based landscape. But, after lessons, when they have more time and can pay attention to the surrounding world, they can appreciate the aesthetic of the campus, the scent of flowers and the song of birds (the individual-based landscape). Finally female students, when cross the campus in the evening feel the hostility of the surroundings (the observer-based landscape), and react selecting the more safety trail.

In a paper titled "Culture, Control, and Perception of Relationships in the Environment" Ji et al. (2000) describe the difference in the environment perception between East Asians (mostly Chinese) and Americans undergraduate students. East Asians have a more holistic vision of the perceived surroundings, while the seconds are more confident on objects. These authors hypothesize that the difference in perception can be strictly related to social environment. Western culture encourages individuals to acquire personal control and autonomy ('primary control'). The Asian culture encourages individuals to adhere to social norms mainly developed in the family context ('secondary control'). The argumentations are aligned to the concept expressed into the observerbased landscape hypothesis.

### The eco-field hypothesis

Recently Farina and Belgrano (2004) have formed the hypothesis that every living function performed by organisms is associated with a specific spatial configuration of their surroundings, and coined the term 'eco-field' to represent this configuration. The eco-field has been considered like an ecological space, or carrier of meaning, in which every living function interacts semiotically with the surrounding world.

In the present contribution the eco-field hypothesis is more broadly discussed to better connect the 'cognitive landscape' model with the principles of 'traditional' landscape ecology. Unlike von Uexküll's *Umwelt*, that represents the junction between 'perceptual' and 'effector' world, the eco-field is a function-specific perceived 'piece of land', that assumes such a spatial configuration as peculiar and distinct character of the organismic-perceived landscape.



Figure 2. Every organism can perceive the spatial configuration meaning carrier in the same location or can find the adapt eco-field in another location.

For every function it performs, like searching food, mating, territorial defending, migrating and roosting, an organism requires an operational space with ecological characteristics to achieve the best performance of the selected function.

We have to assume that for every living organismic function the perceived surroundings change accordingly. The number of eco-fields perceived by an organism is therefore related to the functional complexity of that organism.

Organisms have two principal different possibilities to locate the spatial configurations carriers of meaning: the eco-field spatial configuration to search around, and to find different spatial configurations in the same locality (spatial overlap), or to search some specific spatial configurations in non overlapping locations (spatial distinctiveness) (Figure 2). For instance a spatial overlap of eco-fields can be described for a song-bird like the robin (Erithacus rubecula), that selects wooded areas during the breeding season. The trees are used as a singing sites ('patrolling' eco-field) and the undergrowth to search food ("foraging" ecofield) and to place the nest ("nesting" eco-field). But, for instance, a spatial distinctiveness can be observed in chaffinch (Fringilla coelebs) that needs woodlands to place the nest and to sing, and open areas (fields and grasslands) where to search food.

The eco-field hypothesis is not an absolute conceptual novelty into the panorama of landscape ecology but offers a new interpretation of the complex processes by which organisms interact with a variable environment, see f.i. Hjermann (2000) and Manning et al. (2004). In fact, several studies on the landscape are carried out by using a multiscale framework in order to capture the complexity of processes and patterns observed across a landscape (Hay et al. 2001; Wellnitz et al. 2001). The definition of the landscape as a complex system in which the spatial and temporal scales are both important elements, implicitly assumes that the independent objects have a specific approach in space, time, resources and semiosis (Schooley and Wiens 2001).

# Environmental heterogeneity, the eco-field scoring and the chronosequences

A large portion of landscape ecology focuses on environmental heterogeneity and how this emergence affects processes and species aggregation (see f.i. Turner 1987; Kolasa and Pickett 1991).

Every eco-field can be recognized by a species not as hostile or favorable but more or less valuable. This fuzziness allows a species to adapt the selected living function accordingly (Inglis et al. 2001). This process of surrounding scrutinity is repeated for every living function adopting multiple locally optimal learning strategies (see f.i. the modeling of Kerr and Feldman 2003). For instance, Whittington et al. (2004) have found that tracked wolf (*Canis lupus*) changes path tortuosity according to the more high-use trails, within areas of high-trail and road density, near predation sites, and in rugged terrain.

At the same way, the quality of each eco-field has direct consequences on the individual's fitness, concurring to favour the individuals that have selected the eco-field with the more favourable conditions.

Every living function requires a specific ecofield, but according to the state of life cycle a variability in the spatial configuration perception must also be expected (see Galea et al. 1996). For instance, Bascompte and Vilà (1997) have found a different fractal dimension of wolf path as a function of the season, arguing that this depends on the physiological status (normal, breeding and wandering) and on sex.

This fact opens the road to an interesting experimentation and re-consideration of behavioral models (f.i. Plowright and Gelen 1985). For instance, we can expect the fattest individuals where the density is low and food is abundant. At the same time, individuals could experience a greater predatory pressure and, in this way, the advantage for abundant resources is reduced by the highest predatory pressure.

If this process captures environmental variability, we can explain the phenotypic differences encountered when the populations are closely monitored (Southwick and Buchmann 1995; Norris et al. 2004).

The variability in eco-field quality, is not the only independent factor responsible of individual variability, we have to also consider the chrono-sequence by which a single living function is performed. For instance, in song birds, at sunrise, chorus is genetically fixed, although phenology and other environmental factors, can play an important role. The morning chorus assumes a relevant function in regulating the territoriality, and if a natural or man-made disturbance reduces or prevents such chorus, social consequences on the entire community are expected because chorus can not be repeated later in the day. The chronosequence of the living functions, neglected in most of the ecological investigations, assumes a relevant role in the adaptation of organisms to the environment.

Operationally, for a selected individual or population, a specific region of a mathematical space can be delimited plotting the quality of each ecofield and the position in the chrono-sequence of the related living function. To interpret the meaning of this functional signature the concept of cognitive niche, a niche created by cognitive processes like pattern recognition, memory and learning (Beecham 2001) can be used. And Hoffmeyer (1997) suggested that organisms not only have an ecological niche but also a semiotic niche, 'i.e. they will have to master a set of signs of visual, acoustic, olfactory, tactile and chemical origin in order to survive.'

#### Niche, habitat, Umwelt and eco-field

Niche, habitat, *Umwelt* and eco-field have been elaborated in different periods along ontogenesis of the ecological thought, but are strictly linked each other (Figure 3). Niche is considered the ecological hyper volume composed by the range of variables under which an organism lives. The habitat is the environmental box in which a species is living. Most of the habitat description is based on the vegetation criterion or on geo-pedologicalclimatic criterion. But, as argued by Mitchell and Powell (2003), the definition of habitat as homogeneous patches should be replaced by the depiction of habitat as a 'surface fitness,' 'where the distribution of resources critical to the survival and reproduction of animals is depicted in space.' The Umwelt has been the first attempt to link together animal behavior and the environment. Finally the eco-field explicitly connects the geographical dimension of the habitat (the spatial configuration)



*Figure 3.* Relationships between the three ways in which the information is extracted by the cognitive matrix and the eco-field hypothesis. Some eco-fields are the result of the individual-based landscape cognitive mechanisms, others only use the observer-based landscape mechanism, others the two combined. The neutrality-based landscape, by definition, cannot be connected directly to the eco-field hypothesis.

with the living functions that describes not only the (animal) behavior but also the plant habits. Plants, unlike animals do not have an explicit nervous system, but their semiosis is well developed although less information is available (Kull 2000; Karban 2001; Tscharntke et al. 2001). Plants perform the living function by means of an extraordinary phenotypic plasticity (Grace and Platt 1995). Shape, size and branch numbers are some of the most evident structures that plants change according to the environmental conditions they experience. Measuring plant morphology is the way to look at their eco-fields. Finally, when distribution and diversity of plants are investigated a scaling effect, possibly due to plant eco-fields, can be observed (He et al. 2002).

#### New perspectives opened by eco-field hypothesis

When the organismic-centered-view of the landscape is compared with the vision of a neutral matrix (land mosaic) from which some properties like heterogeneity, resilience and connectivity emerge (Johnson et al. 1992), the two visions seem, at a first sight, divergent, but become operationally complementary.

The eco-field hypothesis can contribute to a better understanding habitat selection in plants and animals (f.i. Cody 1985) investigating the adaptive mechanisms and filling the epistemological gap between ecology, behavior, and cognition.

This hypothesis could be useful to interpret the scaling process in habitat preferences observed in large herbivorous like elk and bison (Wallace et al. 1995) or the adaptive strategies of small mammals when move across a fragmented environment (Diffendorfer et al. 1995).

In the study of connectivity, very popular indeed in ecological conservation, the selection an organismic centered-perspective becomes necessary to improve the efficiency of conservation policies (Keitt et al. 1997). It is the case of the South Florida panthers studied by Kerkhoff et al. (2000). Panthers interact with forest cover at a broad range of spatial scale according to foraging needs, potential access to mates, shelter and impact fitness. If this study were to be revisited using the eco-field hypothesis, clearly would emerge that for every living function panthers search for a specific type of forest cover under a scaled geographic range. And from a generic explanation of a multiscale use of the territory, adopting adequate investigations, could result that every living function (and this is not an easy point to develop), requires a specific eco-field that has, by definition, an inherent scale.

Lima and Zollner (1996) stressed the opportunity to activate studies of behavioral ecology of ecological landscapes and the eco-field hypothesis could be of great utility for interpret the complex mechanisms that regulate the size of colonies in social insects (Crist and Wiens 1994). For instance, the aggregation of desert harvester ant, *Pogonomyrmex barbatus*, to allocate resources to growth, to maintain and to reproduce depends of the several factors, largely unknown (Jun et al. 2003). It would be of great interest to investigate how individuals regulate living functions in order to increase the colonial fitness.

The recognition of a spatial configuration carrier of meaning requires a (cognitive) memory. Recently indirect evidence of the use of spatial memory (to recognize specific eco-field) has been found at neuro-anatomical level in migratory and non migratory populations of *Junco hyemalis* (see f.i. Cristol et al. 2003). The migratory populations resulted with a better spatial memory and denser hippocampal neurons than non migratory co-specifics.

The ecological and evolutionary consequences of the direct modification of organism's surrounding could be a further field of interest in which to find ground for the eco-field hypothesis. For instance, every herbivore influences the vegetation and modifies the grazing patch stimulating the growth of palatable plants. Beavers build dams and voluminous refuges that influence the flux of organisms and nutrients across entire forest ecosystems (Naiman et al. 1988). These processes can be discussed using the perspective of the nicheconstruction (Odling-Smee et al. 2003; Day et al. 2003). The niche construction can be defined like "... the process whereby organisms, through their metabolism, their activities, and their choices, modify their own and/or each other niche' (Odling-Smee et al. 2003: 419). Many organisms can be regarded as 'ecosystem engineers' that modify the surroundings according to specific living functions. Contemporarily, the niche construction creates new environmental conditions, an ecological inheritance for the future generations

assuming that such a phenomenon has a strong (co-)evolutionary valence.

The eco-field performs the role of 'arena' in which such 'engineers' carry out a project according to both genetic and ecological inheriecological inheritance tance. Genetic and (according to Odling-Smee 1988) referes to 'a legacy of a sub-set of natural selection pressure that have been modified by the niche construction of their genetic or ecological ancestors.' The niche construction hypothesis confirms the role of spatial cognitive maps used by organisms like a 'template' to 'build' a favorable spatial configuration. It represents a variant of the eco-field hypothesis in which instead of simply searching for a favorable spatial configuration, organisms self produce, in a selected area (habitat), a configuration driven by a 'cognitive template.'

The eco-field hypothesis could be utilized in the study of human environmental behavior. In the paper of Petherick (2000/01) previously commented, the levels of student's fear on the university campus has been mapped (Figure 7, p. 106). Under the hypothesis of the eco-field, such map represents the reverse image of the 'safety' ecofield. Safety eco-field emerges from the perception of the spatial configuration of bush, trees, roads and buildings when people activate the 'safety' living function (see also Luymes and Tamminga 1995). It is not difficult to extend this reasoning from humans to wild animals and to the way they search for spatial configurations that assure the minor risk from predation ('anti-predatory' ecofield).

Turning back to the traditional landscape ecology paradigms, corridor concept so popular in conservation and landscape management (f.i. Harrison 1992; Simberloff et al. 1992; Andreassen et al. 1996; Naiman and Rogers 1997; Beier and Noss 1998), under the eco-field framework becomes the 'transfer' eco-field. In the same way, homing capacity of pigeons can be revisited in terms of 'homing' eco-field. When displaced, pigeons utilize visual and olfactory cues to select the more direct homing trail, and preview sight of the released site (f.i. Biro et al. 2002) or olfactory experience of home landscape scents (Papi 1991) improve the homing performance.

For these few examples it should be clear that we have not simply exchanged the name of a process with the 'eco-field' word. The eco-field hypothesis admits the shift of perception inside the home range of a species when functions change or when during the performance of a function some controlling variables of that function change in attributes. For instance, if resources become scarce in one location during the foraging activity, such scarcity can elicit either a 're-sampling behavior' in the same locality or a shift into an 'explorative function' causing the displacement of the organism into new foraging area. In both the cases a new perception of the surroundings is performed. If the 'sampling' function is activated landscape is discriminated between exploited and un-exploited paths. But, when the explorative function is adopted the landscape is perceived in terms of paths and friction areas.

### **Concluding remarks**

If we recognize landscape ecology as a 'disciplineintegrating' science, the eco-field hypothesis is part of the developmental strategy of this new science, connecting geographical, cultural, sociological, chorological and ecosystemic approaches with organismic-centered-view of surrounding complexity, and developing an epistemological connection between information, biosemiotics, and evolutionary ecology. The eco-field hypothesis bridges the human use of the 'landscape' across a multi-organismic matrix, opening a new era for 'landscape' experiments, design and conservation.

In this contribution the discussion of the ecofield hypothesis has been carried out especially in the 'traditional' ecology realm.

We recognize the great potentiality of the ecofield hypothesis to investigate, for instance, the environmental preferences of herbivores and these relationships with plants distribution. At the same time, the eco-field could be adopted to model the behavior of predators.We are aware that this is not enough to gain full credit for the "cognitive landscape" approach and that further discussions with geographers, anthropologists, evolutionary biologists, architects, planners, environmental psychologists, ecological behaviorists and social scientists could be extremely beneficial, and eco-field hypothesis ultimately seems a good paradigm to put such confrontation in practice. In particular, the new theoretical approach of the eco-field hypothesis seems extremely useful to investigate the human behavior and the associated environmental preferences that cause most of present-time landscape modifications.

#### References

- Andreassen H.P., Halle S. and Ims R.A. 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. Journal of Applied Ecology 33: 63–70.
- Antrop M. 1998. Landscape change: plan or chaos? Landscape and Urban Planning 41: 155–161.
- Appleton J. 1975. The Experience of Landscape. Wiley and Sons, London.
- Barbieri M. 2001. Has biosemiotics come of age? Review of Semiotics 134: 1–4. Special issue.
- Barbieri M. 2003a. Biology with information and meaning. History and Philosophy of Life Sciences 25: 243–254.
- Barbieri M. 2003b. The Organic Codes. Cambridge University Press.
- Bascompte J. and Vilà C. 1997. Fractals and search paths in mammals. Landscape Ecology 12: 213–221.
- Bastian O. 2001. Landscape ecology toward a unified discipline? Landscape Ecology 16: 757–766.
- Bateson G. 1973. Steps to an Ecology of Mind. Granada, London.
- Baudry J., Burel F., Aviron S., Martin M., Ouin A., Pain G. and Thenail C. 2003. Temporal variability of connectivity in agricultural landscapes: do farming activities helps? Landscape Ecology 18: 303–314.
- Beecham J.A. 2001. Towards a cognitive niche: divergent foraging strategies resulting from limited cognitive ability of foraging herbivores in a spatially complex environment. BioSystems 61: 55–68.
- Beer C.G. 1996. Trial and error in the evolution of cognition. Behavioural Processes 35: 215–224.
- Beier P. and Noss R.F. 1998. Do habitat corridors provide connectivity? Conservation Biology 12: 1241–1252.
- Benhamou S. and Pouchet B. 1996. A comparative analysis of spatial memory processes. Behavioural Processes 35: 113–126.
- Bennett A.T.D. 1996. Do animals have cognitive maps? The Journal of Experimental Biology 199: 219–224.
- Beugnon G., Pastergue-Ruiz I., Schatz B. and Lachaud J-P. 1996. Cognitive approach of spatial and temporal information processing in insects. Behavioural Processes 35: 55–62.
- Bingman V.P. and Able K.P. 2002. Maps in birds: representational mechanisms and neural bases. Current Opinion in Neurobiology 12: 745–750.
- Biro D., Guilford T., Dell'Omo G. and Lipp H.-P. 2002. How the viewing of familiar landscapes prior to release allows pigeons to home faster: evidence from GPS tracking. The Journal of Experimental Biology 205: 3833–3844.
- Bissonette J.A. (ed.) 1997. Wildlife and Landscape Ecology. Effect of Pattern and Scale. Springer, New York.
- Bissonette J.A. and Storch I. (eds) 2003. Landscape Ecology and Resource Management. Island Press, Washington.
- Bourassa S.C. 1990. A paradigm for landscape aesthetics. Environment and Behavior 22(6): 787–812.

- Bourassa S.C. 1991. The Aesthetics of Landscape. Belhaven, London.
- Brumm H. and Todt D. 2002. Noise-dependent song amplitude regulation in a territorial songbird. Animal Behaviour 63: 891–897.
- Cody M.L. 1985. An introduction to habitat selection in birds. In: Cody M.L. (ed.), Habitat Selection in Birds. Academic Press, Orlando FL, pp. 3–56.
- Crist T.O. and Wiens J.A. 1994. Scale effects of vegetation on forager movement and seed harvesting by ants. OIKOS 69: 37–46.
- Cristol D.A., Reynold E.B., Leclerc J.E., Donner A.H., Farabaugh C.S. and Ziegenfus C.W.S. 2003. Migratory darkeyed juncos, *Junco hyemalis*, have better spatial memory and denser hippocampal neurons than no migratory conspecific. Animal Behaviour 66: 317–328.
- Cropley D.H. 1998a. Toward formulating a semiotic theory of measurement information Part 1. Measurement 24: 237–248.
- Cropley D.H. 1998b. Toward formulating a semiotic theory of measurement information – Part 2. Measurement 24: 249– 262.
- Danielson B.J. and Hubbard M.W. 2000. The influence of corridors on the movement behavior of individual *Peromyscus polionotus* in experimental landscapes. Landscape Ecology 15: 323–331.
- Danchin E., Giraldeau L.-A., Valone T.J. and Wagner R.H. 2004. Public information: from noisy neighbors to cultural evolution. Science 305: 487–491.
- Day R.L., Laland K.N. and Odling-Smee J. 2003. Rethinking adaptation. The niche-construction perspective. Perspective in Biology and Medicine 46: 80–95.
- Deely J. 2001. Umwelt. Semiotics 134: 125–135.
- Dicke M. and Bruin J. 2001. Chemical information transfer between plants: back to the future. Biochemical Systematics and Ecology 29: 981–994.
- Diffendorfer J.E., Gaines M.S. and Holt R.D. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon, Microtus*, and *Peromyscus*). Ecology 76: 827–839.
- Dukas R. 1998. Cognitive ecology: Prospects. In: Dukas R. (ed.), Cognitive Ecology. The Evolutionary Ecology of Information Processing and Decision Making. The University of Chicago Press, Chicago, pp. 405–409.
- Edwards G.R., Newman J.A., Parson A.J. and Krebs J.R. 1996. The use of spatial memory by grazing animals to locate food patches in spatially heterogeneous environments: an example with sheep. Applied Animal Behaviour Science 50: 147–160.
- Farina A. 1993. Editorial comment: from global to regional landscape ecology. Landscape Ecology 8: 153–154.
- Farina A. and Belgrano A. 2004. The eco-field: a new paradigm for landscape ecology. Ecological Research 19: 107–110.
- Farina A., Bogaert J. and Schipani I. 2005. Cognitive landscape and information: new perspectives to investigate the ecological complexity. BioSystems 79: 235–240.
- Forman R.T.T. and Godron M. 1986. Landscape Ecology. John Wiley and Sons, New York.
- Forman R.T.T., Sperling D., Bissonette J.A., Clevenger A.P., Cutshall C.D., Dale V.H., Fahrig L., France R., Goldman C.R., Heanue K., Jones J.A., Swanson F.J., Turrentine T.

and Winter T.C. 2003. Road Ecology. Science and Solutions. Island Press, Washington, D.C.

- Galea L.A.M., Kavaliers M. and Ossenkopp K.-P. 1996. Sexually dimorphic spatial learning in meadow voles *Microtus pennsylvanicus* and deer mice *Peromyscus maniculatus*. The Journal of Experimental Biology 199: 195–200.
- Gardner R.H. and O'Neill R.V. 1991. Pattern, process, and predictability: The use of neutral models for landscape analysis. In: Turner M.G. and Gardner R.H. (eds), Quantitative Methods in Landscape Ecology: The Analysis and Interpretation of Landscape Heterogeneity. Springer-Verlag, New York, pp. 289–307.
- Gibson J.J. 1979. The Ecological Approach to Visual Perception. Houghton Mifflin, Boston.
- Gil D. and Gahr M. 2002. The honesty of bird song: multiple constraints for multiple traits. Trends in Ecology and Evolution 17: 133–141.
- Golley F.B. 1993. A History of the Ecosystem Concept in Ecology. Yale University Press, New Haven, USA.
- Goodwin B.J. 2003. Is landscape connectivity a dependent or independent variable? Landscape Ecology 18: 687–699.
- Grace S.L. and Platt W.J. 1995. Neighborhood effects on juveniles in an old-growth stand of longleaf pine, *Pinus palustris*. OIKOS 72: 99–105.
- Gutzwiller K.J. (ed.) 2002. Applying Landscape Ecology in Biological Conservation. Springer, New York.
- Hanski I. 1999. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.
- Hanski I.A. and Gilpin M.E. (eds) 1997. Metapopulation Biology. Ecology, Genetics, and Evolution. Academic Press, San Diego CA.
- Harrison R.L. 1992. Toward a theory of inter-refuge corridor design. Conservation Biology 6: 293–295.
- Hay G.J., Marceau D.J., Dubé P. and Bouchard A. 2001. A multiscale framework for landscape analysis: object-specific analysis and upscaling. Landscape Ecology 16: 471–490.
- He F., LaFrankie J.V. and Bo S. 2002. Scale dependence of tree abundance and richness in a tropical rain forest Malaysia. Landscape Ecology 17: 559–568.
- Healy S. and Braithwaite V. 2000. Cognitive ecology: a field of substance? Trends in Ecology and Evolution 15: 22–26.
- Hirose N. 2002. An ecological approach to embodiment and cognition. Cognitive Systems Research 3: 289–299.
- Hjermann D.O. 2000. Analyzing habitat selection in animals without well-defined home ranges. Ecology 85: 1462– 1468.
- Hobbs R. 1994. Landscape ecology and conservation: moving from description to application. Pacific Conservation Biology 1: 170–176.
- Hobbs R. 1997. Future landscapes and the future of landscape ecology. Landscape and Urban Planning 37: 1–9.
- Hoffmeyer J. 1997. Biosemiotics: toward a new synthesis in biology. European Journal for Semiotic Studies 9: 335–376.
- Inglis I.R., Langton S., Forkman B. and Lazarus J. 2001. An information primacy model of exploratory and foraging behavior. Animal Behaviour 62: 543–557.
- Ingold T. 2000. The Perception of the Environment. Essays in Livelihood, Dwelling and Skill. Routledge, Abingdon, UK.
- Ji L.-J., Nisbett R.E. and Peng K. 2000. Culture, control, and perception of relationships in the environment. Journal of Personality and Social Psychology 78: 943–955.

- Johnson A.R., Wiens J.A., Milne B.T. and Crist T.O. 1992. Animal movements and population dynamics in heterogeneous landscapes. Landscape Ecology 7: 63–75.
- Jordan F., Baldi A., Orci K.-M., Racz I. and Varga Z. 2003. Characterizing the importance of habitat patches and corridors in maintaining the landscape connectivity of a *Pholidoptera transsylvanica* (Orthoptera) metapopulation. Landscape Ecology 18: 83–92.
- Jun J., Pepper J.W., Savage V.M., Gillooly J.F. and Brown J.H. 2003. Allometric scaling of ant foraging trail networks. Evolutionary Ecology Research 5: 297–303.
- Karban R. 2001. Communication between sagebrush and wild tobacco in the field. Biochemical Systematics and Ecology 29: 995–1005.
- Keitt T.H., Urban D.L. and Milne B.T. 1997. Detecting critical scales in fragmented landscapes. Conservation Ecology 1(1): 4 (on line). http://www.consecol.org/vol1/iss1/art4.
- Kerkhoff A.J., Milne B.T. and Maehr D.S. 2000. Toward a panther-centered view of the forests of South Florida. Conservation Ecology 4: 1 (on line). http://www.consecol.org/ vol4/iss1/art1.
- Kerr B. and Feldman M.W. 2003. Carving the cognitive niche: optimal learning strategies in homogeneous and heterogeneous environments. Journal of Theoretical Biology 220: 169–188.
- Kolasa J. and Pickett S.T.A. (eds) 1991. Ecological Heterogeneity. Springer-Verlag, New York.
- Krampen M. 1992. Phytosemiotics revisited. In: Sebeok T.A. and Umiker-Sebeok J. (eds), Biosemiotics. The Semiotic Web 1991. Mouton de Gruyter, Berlin, pp. 213–219.
- Kull K. 1998a. Semiotic ecology: different natures in the semiosphere. Sign Systems Studies 26: 344–371.
- Kull K. 1998b. On Semiosis, Umwelt, and Semiosphere. Semiotics 120. 299–310.
- Kull K. 2000. An introduction to phytosemiotics: Semiotic botany and vegetation sign systems. Sign Systems Studies 28: 326–350.
- Kull K. 2005. A brief history of Biosemiotics. Journal of Biosemiotics 1: 1–34.
- Lima S.L. and Zollner P.A. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution 11: 131–135.
- Liu J. and Taylor W.W. (eds) 2002. Integrating Landscape Ecology into Natural Resource Management. Cambridge University Press, Cambridge.
- Luymes D.T. and Tamminga K. 1995. Integrating public safety and use into planning urban greenways. Landscape and Urban Planning 33: 391–400.
- Mabry K.E. and Barrett G.W. 2002. Effects of corridors on home range sizes and interpatch movements of three small mammal species. Landscape Ecology 17: 629–636.
- MacArthur R.H. and Wilson E.O. 1967. The Theory of Island Biogeography. Princeton University Press, Princeton, N.J.
- Manning A.D., Lindenmayer D.B. and Nix H.A. 2004. Continua and umwelt: novel perspectives on viewing landscapes. Oikos 104: 621–628.
- Matthysen E. 2002. Boundary effects on dispersal between habitat patches by forest birds (*Parus major*, *P. caeruleus*). Landscape Ecology 17: 509–515.
- Merry Uri 1995. Coping with Uncertainty. Praeger, Westport, CT.

- Miller C. and Urban D.L. 2000. Connectivity of forest fuels and surface fire regime. Landscape Ecology 15: 145–154.
- Milne B.T. 1992. Spatial aggregation and neutral models in fractal landscapes. American Naturalist 139: 32–57.
- Mitchell M.S. and Powell R.A. 2003. Linking fitness landscape with the behavior and distribution of animals. In: Biossonette J.A. and Storch I. (eds), Landscape Ecology and Resource Management Linking Theory with Practice. Island Press, Washington, pp. 93–124.
- Naiman R.J. and Rogers K.H. 1997. Large animals and systemlevel characteristics in river corridors. BioScience 47: 521– 529.
- Naiman R.J., Johnston C.A. and Kelley J.C. 1988. Alteration of North American streams by beaver. BioScience 38: 753–762.
- Nassauer J.I. 1995. Culture and changing landscape structure. Landscape Ecology 10: 229–237.
- Naveh Z. 1995. Interactions of landscapes and cultures. Landscape and Urban Planning 32: 43–54.
- Naveh Z. 2000. Introduction to the theoretical foundations of multifunctional landscape and their application in transdisciplinary landscape ecology. In: Brandt J. and Trees B. (eds), Multifunctional Landscapes. Interdisciplinary Approaches to Landscape Research and Management. Centre for Landscape Research, Roskilde, DK pp.27–43.
- Naveh Z. and Lieberman A. 1984. Landscape Ecology. Springer-Verlag, New York.
- Nicholls C.I., Parrella M. and Altieri M.A. 2001. The effects of a vegetational corridor on the abundance and dispersal of insect biodiversity within a northern California organic vineyard. Landscape Ecology 16: 133–146.
- Norris D.R., Marra P.P., Montgomerie R., Kyser T.K. and Ratcliffe L.M. 2004. Reproductive effort, molting latitude, and feather color in a migratory songbird. Science 306: 2249– 2250.
- Nöth W. 2005. Semiotics for biologists. Journal of Biosemiotics 1: 183–198.
- Odling-Smee F.J. 1988. Niche constructing phenotypes. In: Plotkin H.C. (ed.), The Role of Behavior in Evolution. MIT Press, Cambridge, Mass.
- Odling-Smee F.J., Laland K.N. and Feldman M.W. 2003. Niche Construction. The Neglected Process in Evolution. Princeton University Press, Princeton, NJ.
- Odum E.P. 1977. The emergence of ecology as a new integrative science. Science 195: 1289–1293.
- O'Neill R.V. 1999. Theory in landscape ecology. In: Wiens J.A. and Moss M.R. (eds), Issues in Landscape Ecology. Pioneer Press of Greely, Inc., Greely Colorado, pp. 1–5.
- O'Neill R.V. 2001. Is it time to bury the ecosystem concept? (with full military honors, of course!). Ecology 82(12): 3275– 3284.
- Papi F. 1991. Olfactory navigation. In: Perthold P. (ed.), Orientation in Birds. Birkhäuser Verlag, Basel, pp. 52–85.
- Petherick N. 2000/01. Environmental design and fear: the prospect-refuge model and the University College of the Cariboo Campus. Western Geography 10(11): 9–112.
- Pickett S.T.A. and Cadenasso M.L. 1995. Landscape ecology: spatial heterogeneity in ecological systems. Science 269: 331–334.
- Plowright R.C. and Galen C. 1985. Landmarks or obstacles: the effects of spatial heterogeneity on bumble bee foraging behavior. OIKOS 44: 459–464.

- Reinhard J., Srinivasan M.V. and Zhang S. 2004. Scent-triggered navigation in honeybees. Nature 427: 411.
- Real L.A. 1993. Toward a cognitive ecology. Trends in Ecology and Evolution 8: 413–417.
- Risser P.G. 1989. The movement of nutrients across heterogeneous landscapes. In: Clarholm M. and Bergstrom L. (eds), Ecology of Arable Land. Kluwer Academic Publishers, Dordrecht, pp. 247–251.
- Risser P.G., Karr J.R. and Forman R.T.T. 1984. Landscape ecology: directions and approaches. Illinois Natural History Survey. Special Pubblication Number 2, Champaign.
- Schooley R.L. and Wiens J. 2001. Dispersion of kangaroo rat mounds at multiple scales in New Mexico, USA. Landscape Ecology 16: 267–277.
- Sebeok T.A. 1972. Perspectives in Zoosemiotics. Mouton, The Hague.
- Sebeok T.A. 1995. Semiotics and the biological sciences: initial conditions. Discussion Paper No. 17. Collegium Budapest/ Institute for Advanced Study.
- Sebeok T.A. and Umiker-Sebeok J. (eds) 1991. Biosemiotics. The Semiotic Web 1991. Mouton de Gruyter, Berlin.
- Sharov A.A. 1998. Towards the semiotic paradigm in biology. Semiotics 120: 403–419.
- Shettleworth S.J. 2001. Animal cognition and animal behavior. Animal Behaviour 61: 277–286.
- Simberloff D., Farr J.A., Cox J. and Mehlman D.W. 1992. Movement corridors: conservation bargains or poor investment? Conservation Biology 6: 493–504.
- Southwick E.E. and Buchmann S.L. 1995. Effects of horizon landmarks on homing success in honey bees. American Naturalist 146: 748–764.
- Stauffer D. 1985. Introduction of Percolation Theory. Taylor and Francis, London.
- Stonier T. 1990. Information and the Internal Structure of the Universe. An Exploration into Information Physics. Springer-Verlag, Berlin.
- Stonier T. 1996. Information as a basic property of the universe. BioSystems 38: 135–140.
- Tress B., Tress G., Décamps H. and d'Hauteserre A.-M. 2001. Bridging human and natural sciences in landscape research. Landscape and Urban Planning 57: 137–141.
- Tscharntke T., Thiessen S., Dolch R. and Boland W. 2001. Herbivory, induced resistance, and interplant signal transfer in *Alnus glutinosa*. Biochemical Systematics and Ecology 29: 1025–1047.
- Turner M.G. (ed.) 1987. Landscape Heterogeneity and Disturbance. Springer-Verlag, New York.
- Turner M.G. 1989. Landscape ecology: the effect of pattern on process. Annual Review of Ecology and Systematics 20: 171–197.
- Turner M.G., Gardner R.H. and O'Neill R.V. 2001. Landscape Ecology in Theory and Practice. Pattern and Process. Springer-Verlag, New York.
- Uexküll J. von 1940 (1982). The theory of meaning. Semiotics 42(1): 25–82.
- Uexküll J. von 1934 (1992). A stroll through the worlds of animals and men: a picture book of invisible worlds. Semiotics 89(4): 319–391.
- Ulrich R.S. 1983. Aesthetic and affective response to natural environment. In: Altman I. and Wohlwill J.F. (eds), Behavior and Natural Environment. Plenum Press, New York, pp. 85– 125.

- Wallace L.L., Turner M.G., Romme W.H., O'Neill R.V. and Wu Y. 1995. Scale of heterogeneity of forage production and winter foraging by elk and bison. Landscape Ecology 10: 75– 83.
- Ward D. and Saltz D. 1994. Foraging at different spatial scales: Dorcas gazelles foraging for lilies in the Negev desert. Ecology 75: 48–58.
- Wellnitz T.A., LeRoy Poff N., Cosyleon G. and Steury B. 2001. Current velocity and spatial scale as determinants of the distribution and abundance of two rheophilic herbivorous insects. Landscape Ecology 16: 111–120.
- Whittington J., St Clair C.C. and Mercer G. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. Ecology and Society 9(1): 4 (on line).
- Wickler W. 1971. Mimikry. Kindler, München.
- Wiens J.A. 1992. What is landscape ecology, really? Landscape Ecology 7: 149–150.

- Wiens J.A. 1995. Landscape mosaics and ecological theory. In: Hansson L., Fahrig L. and Merriam G. (eds), Mosaic Landscapes and Ecological Processes. Chapman and Hall, London, pp. 1–26.
- Wiens J., Stenseth N.C., Van Horne B. and Ims R.A. 1993. Ecological mechanisms and landscape ecology. OIKOS 66: 369–380.
- With K.A. and Crist T.O. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446–2459.
- Wu J. and Hobbs R. 2002. Key issues and research priorities in landscape ecology: an idiosyncratics synthesis. Landscape Ecology 17: 355–365.
- Wu J. and Marceau D. 2002. Modeling complex ecological systems: an introduction. Ecological Modelling 153: 1–6.
- Ziff R. 1986. Test of scaling exponents for percolation-cluster perimeters. Physical Review Letters 56: 545–548.
- Zonneveld I.S. 1995. Land Ecology. SPB Academic Publishing, Amsterdam.