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A QUESTION OF SCALE: THE EFFECTS OF ENVIRONMENTAL HETEROGENEITY ON POPULATIONS

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Abstract. The focus is on complex landscapes and in these on the effects of hierarchical arrangements and scales on the process. Rightfully considered a philosophical essay in landscape ecology, the paper emphasizes that for a best resolution of domains, of patterns and of their determinants study designs must accommodate scales. Relevant references and examples enrich the contents.

Introduction

The world is composed of landscapes, or spatial mosaics of heterogeneous elements. Landscape ecology considers the ecological effects of spatial heterogeneity, often on the scale of tens of metres to kilometres (Ims 1990, Irlandi 1994, Kotliar & Wiens 1990, Pickett & Cadenasso 1995, Wiens et al. 1993). Spatial heterogeneity can affect a broad range of ecological phenomena, including foraging movements, home range use, dispersal and habitat selection, competition, predation, population and metapopulation dynamics, community structure, and the flow of energy through ecosystems (Johnson et al. 1992, Kolasa & Rollo 1991, Kotliar & Wiens, Lima & Zollner 1996, Wiens et al. 1993). To date, empirical tests and models of these effects have mostly been concerned with the dynamics of mobile organisms in terrestrial ecosystems (Wiens et al. 1993).

The discipline of landscape ecology began in central Europe in the 1960's as a fusion of ideas from human geography, land management, landscape architecture, and holistic ecology (Wiens et al. 1993), and evolved separately in North America from system ecology (Ims 1990). Because of its disparate and relatively recent origins, the field suffers from inconsistent use of terminology and application of concepts (e.g., Norton & Lord 1990, Wiens 1989a, Wiens 1990) and as yet lacks a unified theoretical framework or an established methodology (Ims 1990). Nevertheless, this emerging discipline is relevant to all ecologists, because it explicitly addresses the roles that heterogeneity and spatial scale play in ecological processes.

Environmental heterogeneity: a hierarchical approach

An environment is heterogeneous if a particular qualitative or quantitative descriptor varies among locations (Kolasa & Rollo 1991). Often, environments are described as 'patchy', or containing discrete, internally homogeneous subunits embedded in some sort of matrix that is different from the patch (Forman & Godron 1986, Wiens et al. 1993). Real landscapes, however, are hierarchical mosaics of patches nested within patches, and are heterogeneous over a range of scales (Kotliar & Wiens 1990). For any landscape, several different patch criteria and definitions could be applied. The choice of patch definition determines the scale of environmental heterogeneity under consideration: the smaller the patch, the finer the scale at which the environment is considered heterogeneous. The appropriate scale will depend on the questions asked, the organisms studied, and the time periods considered (Wiens et al. 1993). For example, in a study of nectivorous animals, a patch could be defined as a single flower, an inflorescence or a clump of plants (Pyke 1981, Kotliar & Wiens 1990), depending on the objectives of the study.

Once a scale of heterogeneity has been defined, landscape features that are ecologically relevant can be mapped and quantified. Measurable features of a landscape include the size, shape, number and distribution of patches; the continuity and thickness of patch boundaries; connectivity of patches; contrast between patch and non-patch; the richness and evenness of different patch types, etc. (Wiens et al. 1993). These features can be categorized as describing the *composition* (i.e., the number and types of elements) or the *physiognomy* (i.e., the spatial pattern) of a landscape (Dunning et al. 1992). Recent approaches to characterizing landscape heterogeneity have used fractal geometry to determine a scale-independent index of complexity (Kolasa & Rollo 1991). Patterns in nature behave as fractals when they exhibit self-similarity at all scales (Crist et al. 1992), and retain their complexity when dissected into infinitely small scales (Kolasa & Rollo 1991, With 1994). An index known as the fractal dimension describes the overall complexity of the pattern regardless of scale (With 1994). Because fractal analysis assesses pattern structure across a range of scales (Milne 1991, With 1994), it is uniquely suited to modeling the effects of environmental heterogeneity on a variety of processes (e.g., Crist et al. 1992; Loehle 1990, 1994; Milne 1991; With 1994; but see Gautestad & Mysterud 1994).

Perception of heterogeneity: grain and extent

The amount and type of information an animal receives about its environment will affect movements within a patch, as well as decisions to stay or move from a patch (Bell 1991, Dusenbery 1989, Johnson et al. 1992). The range of scales at which an organism can perceive and respond to environmental heterogeneity can be defined as its *perceptual range* (Kolasa & Rollo 1991, Lima & Zollner 1996). The components of perceptual range are *grain size* (the finest component of the environment that can be differentiated at the shortest distance) and *perceptual extent* (the distance at which an object can be distinguished from a fixed vantage point). We tend to think of perceptual range as a visual phenomenon, but the concepts of perceptual range, perceptual extent and grain size can apply to all sensory modalities.

Grain size sets the lower limit on the scale at which heterogeneity is perceptible; perceptual extent sets the upper limit (Kolasa & Rollo 1991, With 1994). For a given species, perceptual range can be broad or narrow, high or low. In general, small organisms have low perceptual ranges compared to large species, and organisms in simple environments have narrow perceptual ranges compared to those in complex environments. For an individual, grain size and perceptual extent can vary depending on time of day, environmental conditions, and whether the animal is moving or stationary (Kolasa & Rollo 1991, Kotliar & Wiens 1990, With 1994). Movement reduces grain size and increases perceptual extent, permitting the moving animal to perceive heterogeneity in its environment at a range of scales. This phenomenon explains the utility of saltatory search (O'Brien et al. 1989): an animal searching for patches of resources moves at a rate appropriate to sampling a higher scale of heterogeneity, but slows down to locate resources distributed within the patch at a lower scale of heterogeneity (Kolasa & Rollo 1991, With 1994). Despite the importance of perceptual range to ecological questions, relatively few studies have tested how far away an animal can detect a particular landscape element (Lima & Zollner 1996). Yellow-bellied pond slider turtles (*Trachemys scripta*) can detect the presence of water at least 300 m away, using polarized light (Yeomans 1995). In contrast, white-footed mice (*Peromyscus leucopus*) are unable to locate forested habitat only 30 m away (Lima & Zollner 1996).

What is the relationship between perceptual range and landscape ecology? The way environmental heterogeneity is perceived and interpreted determines the scale at which spatial patterns are ecologically relevant to that organism. In the hierarchical array of patchiness in a landscape, an organism cannot respond to levels of heterogeneity that fall outside its perceptual range. Within its perceptual range, an organism's response to certain scales of environmental heterogeneity depends on the context (With 1994). For example, the fine-scaled heterogeneity important to foraging decisions probably will be ignored during long-range movements among patches (Crist et al. 1992, Kolasa & Rollo 1991, Wiens et al. 1993).

Perceptual range ultimately affects ecological phenomena beyond the level of the individual, such as responses to competition and predation, colonization rates, population stability and metapopulation dynamics (e.g., Turchin 1991). For example, species with high perceptual ranges may be influenced by conspecific attraction more than species with low perceptual ranges (e.g., Ray et al. 1991, Reed & Dobson 1993, Smith & Peacock 1990). Effects at boundaries of patches, such as edge hardness, may limit dispersal in species with low perceptual ranges more than in species with high perceptual ranges, because of their relative abilities to detect suitable habitat beyond the boundary of the patch (Lima & Zollner 1996). Species with broad perceptual ranges may be less vulnerable to habitat fragmentation than species with narrow perceptual ranges.

Consequences of heterogeneity: landscape complementation and supplementation

Organisms respond to some scales of environmental heterogeneity in order to locate resources such as food, refuge, and mates (Bell 1991). An animal may leave a resource patch to seek a substitutable resource (e.g., moving from one food patch to another), or a non-substitutable resource (e.g., moving from a food patch to a roost site). The ability of animals to move among resource patches will depend on several features of the landscape, such as patch distribution, boundary characteristics, and the presence of corridors among patches. Landscape supplementation and complementation occur when organisms can move among patches to exploit substitutable and non-substitutable resources, respectively (Dunning et al. 1992). Both processes are likely to occur when resource patches are close together, so that the risks associated with travel time and inefficiency of searching for patches are minimized.

Landscape supplementation occurs when organisms use nearby patches of the same type of habitat to obtain resources found on a focal patch, or to obtain alternative resources (e.g., prey items of a different species) from a different habitat type (Dunning et al. 1992). Species of birds, such as barred owls (*Strix varia*) and pileated woodpeckers (*Drycopus pileatus*), that are usually restricted to large woodlots may occupy small patches in a fragmented landscape if they can forage in nearby patches of woodland habitat (Whitcomb et al. 1977). The persistence of red squirrels (*Sciurus vulgaris* L.) in a fragmented habitat depends on the distances among woodlots (van Apeldoorn et al. 1994), because squirrels forage in more than one woodlot when resource levels are low. Bluegills (*Lepomis macrochirus*) maximize their foraging rates when feeding in open water (Werner et al. 1983a), but in the presence of predatory bass (*Micropterus salmoides*), the smallest size class of bluegills feed in pond vegetation where they are safe from predation (Werner et al. 1983b). Thus, the spatial arrangement of pond vegetation affects the response of the population to varying predation risk. Habitat supplementation may decrease the probability of local extinction. At moderate population densities, female cotton rats (*Sigmodon hispidus*) occupied eight different microhabitats, whereas males were confined to one type (patches dominated by *Rubus sp.*). At the end of a population decline, all survivors (male and female) occupied *Rubus*-dominated patches (Lidicker et al. 1992).

The displacement of individuals by conspecifics into sub-optimal habitats can be considered an effect of landscape supplementation (Dunning et al. 1992). At high population densities, male red-winged blackbirds (*Agelaius phoeniceus*) compete for breeding territories and some are forced to settle in low-quality habitats such as cropland (Clark & Weatherhead 1987). Yearling blackbirds (*Turdus merula*) occupy smaller habitat patches, and experience lower reproductive success than do adults (Møller 1995). Dunning et al. (1992) argue that the presence of low-quality habitats increases the population size that the landscape can support, but their implicit comparison is to a landscape composed of high-quality patches separated by entirely unsuitable habitat. Other authors interpret the effects of sub-optimal habitats on population size from a different perspective. Male willow warblers (*Phylloscopus trochilus*) dispersed non-randomly away from a highway carrying heavy traffic (Foppen & Reijnen 1994). The sub-optimal habitat close to the road supported lower densities of birds than habitat further from the road, and was occupied primarily by yearling males who experienced relatively low reproductive success (Reijnen & Foppen 1994). These authors conclude that these patches reduced, rather than increased, the size of the population in this fragmented landscape.

A high degree of landscape complementation permits a landscape to support a larger population than a landscape in which these resource patches are widely separated (Dunning et al. 1992). For example, fish in a salt marsh may feed in the marsh but retreat to tidal streams that become predator-free ponds at low tide. The largest fish populations are found in areas of the marsh close to streams with refuge pools at low tide (McIvor & Odum 1988). Because pre-diapause larvae of checkerspot butterflies (*Euphydryas editha*) need cooler conditions than post-diapause larvae and pupae (Weiss et al. 1988), populations persist best in regions of the landscape with high topographic relief, where warm and cool hillsides are in proximity.

Source/sink relationships: population fluxes in landscapes

Productive habitat patches may be sources of emigrants, which disperse to less productive patches called sinks (e.g., Buechner 1989, Lidicker 1975). Population size in a source/sink landscape can be affected by landscape composition (Pulliam & Danielson 1991). In simulations, the addition of a small amount of sink habitat increases total population size, but increasing the ratio of sink to source habitat drives the population size down, because high-quality patches become increasingly difficult for dispersers to find. Blondel et al. (1992) demonstrated how the quality of a habitat patch depends on the context of other patches within the landscape. In a study of blue tits (*Parus caeruleus* L.) the authors measured food abundance in two habitat patches on a mainland, and in one isolated patch on an island. Habitat quality was similar between the island habitat and one of the mainland patches, with higher quality on the other mainland patch. On the mainland, the high-quality habitat produced many fledglings that emigrated to the poor-quality patch, which functioned as a sink. On the island, however, birds adjusted their laying dates to maximize production in poor-quality habitat. Thus, availability of different types of habitats to the mainland population resulted in different population dynamics in the island and mainland populations.

Habitat fragmentation: a model for landscape-level processes

Many habitats are increasingly fragmented due to activities such as logging and clearing of land for agricultural use. Fragmented habitats are ideal systems for examining the effects of large-scale environmental heterogeneity. Forest fragmentation may be the underlying cause for declines in populations of migrant birds. In North America, habitat fragmentation is associated with high rates of nest predation and brood parasitism by brown-headed cowbirds (*Molothrus ater*; Robinson et al. 1995). In Sweden, forest fragmentation resulted in increased nest predation by corvids (*Corvus sp.*). Studies of how species respond to habitat fragmentation are crucial in the development of conservation strategies.

Fragmented habitats give rise to metapopulations. Metapopulations are spatially structured populations consisting of subpopulations, separated by space or barriers and connected by dispersal movements (Odam 1991). In fragmented habitats, local populations may go extinct, but the fragment may be recolonized by dispersers moving through habitat corridors. In general, local extinction rate depends on fragment size, whereas the recolonization rate is related to the degree of isolation (Odam 1991). Occurrence of subpopulations in fragments depends both on the dispersal and colonizing ability of the species (Villard & Taylor 1994), and on density and position of corridors (i.e., the degree of 'landscape resistance'; Odam 1991). The presence of corridors increased the number of male meadow voles (*Microtus pennsylvanicus*) dispersing between habitat patches compared to dispersal between unconnected patches in experimental plots. Plots with unconnected patches supported lower population densities than plots with habitat corridors (La Polla & Barrett 1993).

Elements of the landscape can function as barriers to dispersal and affect metapopulation dynamics. Ultimately, barriers to dispersal may lead to reproductive isolation and genetic differentiation of the subpopulations due to genetic drift. White-footed mice in a woodlot that was bisected by a road did not move between patches, even though movements next to the road were frequent and long enough to cross the road (Merriam et al. 1989). Analysis of electrophoretic variants of salivary amylase did not reveal genetic differentiation between the subpopulations on either side of the road.

Shifts in scale

A challenge for ecologists studying heterogeneity is to determine the appropriate scale of investigation (Carlile et al. 1989, Johnson et al. 1992, Kurki & Linden 1995, Wiens 1989a). Tests of theoretical models are highly sensitive to scale, and deviations from theoretical predictions may be due in part to unmeasured heterogeneity at another scale. For example, failure of a patch choice model to predict inflorescence choice by hummingbirds (*Selasphorus platycercus* and *S. rufus*) based on inflorescence size might be due to patchiness of inflorescences at higher scales (Pyke 1981). At a fine scale, spatial associations between least auklets (*Aethia pusilla*) and their zooplanktonic prey are weak, ephemeral, and inconsistent with predictions of optimal foraging. However, patterns of dispersion that correlate with foraging behaviour are evident at higher scales (Russel et al. 1992).

Shifts in scale can cause some patterns to disappear, and new patterns to emerge. At a large scale (100 km^2), the proportion of black grouse (*Tetrao tetrix*) hens with a brood was correlated negatively with the proportion of agricultural land in a forest landscape, presumably due to the high density of generalist predators in a fragmented landscape. At a smaller scale (10.8 km^2), the probability of an observed hen having a brood was higher in the vicinity of agricultural land, probably due to differences in the microhabitats selected by breeding and non-breeding hens (Kurki & Linden 1995). This example illustrates how the broad-scale effect of predation can override local effects of habitat selection. Least flycatchers (*Empidonax minimus* Baird & Baird) negatively influence the distribution of American redstart (*Setophaga ruicila* L.) territories at the scale of 4 ha plots. At a regional scale, however, these species are associated positively (Sherry & Holmes 1988). In this situation, the broad-scale effect of habitat selection compensated for local effects of competition.

Scales of investigation: advantages and limitations

The sample of empirical studies presented here represents the range of scales at which the ecological consequences of spatial heterogeneity are being studied. Fine-scale (i.e., patch-level) studies of heterogeneity can lend themselves to formal tests of hypotheses, because resolution of detail is high and the possibility exists for experimental manipulation and replication. However, the effects of sampling error may be high, and the potential for deriving generalizations is low (Wiens 1989a). Broad-scale (i.e., landscape-level) studies tend to be descriptive and correlative, because the opportunity for manipulation or replication is minimal (Hargrove & Pickering 1992, Wiens 1989a). However, the effects of sampling error are low and the potential for deriving generalizations is high (Wiens 1989a). The integration of findings from various scales will ultimately increase our understanding of the effects of heterogeneity on ecological processes.

The effects of scale and heterogeneity are important to all ecologists, theoreticians and empiricists alike. By observing patterns in heterogeneous environments, ecologists can gain insight into how ecological processes are integrated over a range of scales. For example, concepts formerly in the domain of behavioural ecology, such as animal movements, dispersal and habitat selection are being applied to the study of the dynamics and distribution of populations in heterogeneous landscapes (Lima & Zollner 1996). Not all studies can address how ecological processes vary over multiple scales of environmental heterogeneity. However, studies conducted at several scales will provide the best resolution of domains, of patterns and their determinants (Wiens 1989a).

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