

Spatial Ecological Hierarchies: Coexistence on Heterogeneous Landscapes via Scale Niche Diversification

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Abstract

Spatially heterogeneous environments are generally characterized by nested landscape patterns with resource aggregations on several scales. Empirical studies indicate that such nested landscape patterns impose selection constraints on the perceptive scales of animals, but the underlying selection mechanisms are unclear. We investigated the selection dynamics of perceptive scale within a spatial resource utilization model, where the environment is characterized by its resource distribution and species differ in their perceptive scales and resource preemption capabilities. Using three model landscapes with various resource distributions, we found that the optimal perceptive scale is determined by scale-specific attributes of the

INTRODUCTION

From the viewpoint of a hierarchical concept of ecosystems, natural biological systems are comprised of a hierarchy of structures and processes, where no specific level in the system can respond stably to all scales of perturbation, but each level is homeorhetic relative to fluctuations on a specific scale (O'Neill and others 1986; Allen and Hoekstra 1992; Wu and Loucks 1995). Accordingly, a community of species that performs ecological functions on distinct scales can be regarded as a spatial ecological hierarchy. In conjunction with functional diversity within scales, such a functional redun-

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landscape pattern and that the number of coexisting species increases with the number of characteristic scales. Based on the results of this model, we argue that resource aggregations on different scales act as distinct resources and that animal species of particular perceptive scales are superior in utilizing resource aggregations of comparable spatial extent. Due to the allometric relationship between body size and perceptive scale, such fitness difference might result in discontinuous body mass distributions.

Key words: scaling; body size; textural discontinuity; competition; niche; perceptive scale.

dancy across scales may enhance ecosystem resilience (Peterson and others 1998). We tested a mechanistic explanation for the emergence of such spatial ecological hierarchies and considered its implications for observed discontinuous body mass distributions.

Scale attributes of spatial environmental structure have profound effects on ecosystem dynamics (Levin 1992). Landscape patterns—that is, the spatial pattern of environmental variables—are formed by several biotic and abiotic processes acting on distinct spatial and temporal scales, ranging from slight daily fluctuations through disturbances of intermediate size and frequency to large-scale, infrequent events (Clark 1985; Krummel and others 1987; Menge and Olson 1990). The overall effect of these cross-scale processes produces nested

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landscape patterns with coarser or finer differences in environmental conditions on larger or smaller scales, respectively (Delcourt and Delcourt 1988; Kotliar and Wiens 1990; Forman 1995). According to the extended keystone hypothesis, each ecosystem is controlled by a small number of structuring processes (Holling 1992). It is reflected in both spatial and temporal periodicities of environmental factors at distinct frequencies. Periodic patterns at particular scales can be detected from vegetational and topographic data, and in many cases the underlying structuring processes are identifiable (McNamee and others 1981; Romme 1982; Franklin and Forman 1987; Malamud and others 1998; Dale 1999).

Empirical studies indicate that there is a corresponding hierarchy for the ecological characteristics of communities. Observed discontinuous body size distributions suggest that landscape-scale attributes impose selection constraints on animals (Kolasa 1989; Restrepo and others 1997; Smith and others 1997; Lambert and Holling 1998; Allen and others 1999; Raffaelli and others 2000). The allometric relationship between animal size and home range provides a way to convert body mass distributions to spatial metrics, and thus to express the perceptive scales of different-sized species (McNab 1963; Harestad and Bunnell 1979; Reiss 1988). "Perceptive scale" is the size of the window used to view the world by individuals. Both spatial extent and resolution change with perceptive scale, and observed patterns of the environment shift accordingly. Species with a large perceptive scale travel through a larger area during a given time interval, enabling them to consume resources from a larger area, but they cannot perceive small-scale heterogeneities, due to the shorter time they spend at any given location.

The textural discontinuity hypothesis proposes that the existence of a hierarchical landscape structure is reflected by a discontinuous distribution in the size of animals and their corresponding perceptive scales (Holling 1992). According to this concept, animals of various perceptive scales are sensitive to landscape features of different spatial extent; the number of species with different body sizes and perceptive scales reflects the amount of resources available at particular scales (see also Allen and Saunders 2002).

A critical assumption underlying the textural discontinuity hypothesis is that selection acts on perceptive scale, favoring species that perceive and respond to the "most appropriate" scales of resource heterogeneity. Precisely how this occurs in nature is unclear, but lessons learned from previ-

ous research provide some clues. There is strong empirical evidence to show that the fitness of individuals depends largely on perceived spatial variance as the animals spot resource-abundant sites during their movement over the landscape (Hildén 1965; Pyke 1981; Morris 1987; Senft and others 1987). The experience of environmental variance decreases with increasing perceptive scale (Carlile and others 1989; Moloney and others 1992), suggesting that small perceptive scale, which implies small body size, is superior. However, due to the allometric relationship between perceptive scale and body size, the quality of environmental perception is in trade-off with several other traits, including predator avoidance, nutrient utilization, and size-related competition ability (Persson 1985; Dickman 1988; Thompson and Fox 1993). Consequently, we must investigate perceptive scale in the context of other traits.

No one has yet explored the foregoing critical assumption of Holling's (1992) hypothesis. In this paper, we study the effect of natural selection on perceptive scale within a simple resource utilization model. To investigate the selection dynamics of interdependent traits in its simplest form, we consider the case of two traits: perceptive scale and resource preemption capability. We claim that the selectional effects of environmental perception depend on the pattern of landscape structure within and across scales, whereas this does not hold for other traits. Depending on the underlying environmental heterogeneity, fitness difference might introduce discontinuities in the distribution of traits within an animal community. Given a nested landscape pattern, we might expect a multimodal distribution of perceptive scale and body size among species, owing to the allometric relationship between them.

Methods

We use a spatial resource utilization model that simulates population dynamics of competing species that consume the same resource but differ in their perceptive scales and competitive abilities. To avoid boundary effects, the model landscape is a string of habitable sites with periodic boundary conditions. Each site *i* is characterized by its resource density r_i ($i \in \{1, 2, ..., L\}$) and local population densities p_{ix} ($i \in \{1, 2, ..., L\}$) and local population densities p_{ix} ($i \in \{1, 2, ..., L\}$, $x \in \{1, 2, ..., X\}$) of each species *x*, where L = 256 denotes the number of sites and X = 70 is the number of species. Due to periodic boundary conditions, $r_{i\pm L} = r_i$ and $p_{i\pm Lx} = p_{ix}$.



Figure 1. Resource patterns of three model landscapes. Average resource level is equal on all three model landscapes, but it is distributed differently. **a** Homogeneous landscapes. **b** Simple heterogeneous landscape showing heterogeneity on one scale with resource aggregations of size $\sigma = 32$. **c** Nested landscape pattern, showing heterogeneity on three scales, with resource aggregations of size $\sigma_1 = 8$, $\sigma_2 = 32$, and $\sigma_3 = 128$.

Local populations are sets of individuals feeding within a home range that is centered on a particular site.

Model Landscapes

Resource density r_i expresses the abundance of available resources on particular sites. It is constant over time, but varies with spatial location *i*. We consider three model landscapes with specific resource distributions $r_i^{\text{I}}, r_i^{\text{II}}$, and r_i^{III} (Figure 1). The mean value of the resource level is C = 1 in all three cases. The homogeneous model landscape has uniform resource distribution $r_i^{\rm I}$. It will be used as a benchmark for comparisons with two heterogeneous model landscapes. The simple heterogeneous landscape has a square wave resource distribution r_i^{II} . The third, nested model landscape has resource distribution $r_i^{\text{III}} = r_i^{\text{IIIa}} + r_i^{\text{IIIb}} + r_i^{\text{IIIc}}$ that is the superimposition of three (a, b, c) square wave functions with mean values of C_1 , C_2 , and C_3 (for details, see Appendix at http://www.springerlink.com).

We define the scale of a pattern, denoted by σ , as the size of resource aggregations. Obviously, a homogeneous pattern has no characteristic scale, or it is infinite in a strict sense. The scale of the simple heterogeneous landscape is $\sigma = 32$, equal to the half-period of the square wave function r_i^{II} . The third, nested landscape, representing an environment formed by several structuring processes, exhibits heterogeneities on three scales. These $\sigma_1 = 8$, $\sigma_2 = 32$, $\sigma_3 = 128$ values correspond to half-periods of r_i^{IIIa} , r_i^{IIIb} , and r_i^{IIIc} , respectively.

Perceptive Scale and Pattern Intensity

Species differ in their perceptive scales—that is, in terms of the spatial scale at which they perceive and utilize resources and average environmental heterogeneities. Species x has a perceptive scale of $S_x = 2x - 1$ sites. Species x = 1 has the smallest perceptive scale of $S_1 = 1$, having access to resources in only one site. Species x = X has maximal perceptive scale of $S_x = 2X - 1$, with access to resources in 2X - 1 sites. Generally, the resource uptake region of a local population p_{ix} starts at i - x + 1 and ends at i + x - 1. Resource consumption activity of individuals is distributed evenly within this spatial range; thus the experienced resource level of an individual of species x on site i is:

$$\bar{r}_{ix} = \sum_{l=i-(x-1)}^{i+x-1} r_l / (2x-1)$$
(1)

Perceptive scale determines the ability of a species to differentiate between favorable and unfavorable sites. This ability can be expressed by the difference between highest and lowest experienced resource levels as a function of perceptive scale:

$$I(S_x) = max\{\bar{r}_{1x}, \bar{r}_{2x}, \dots, \bar{r}_{Lx}\} - min\{\bar{r}_{1x}, \bar{r}_{2x}, \dots, \bar{r}_{Lx}\}$$
(2)

This quantity is often referred to as "pattern intensity" (Dale and MacIsaac 1989). Hereafter, we will denote intensity functions of the three model landscapes by I^{I} , I^{II} , and I^{III} , respectively.

Population Dynamics

The concept of population dynamics used in our study is derived from the Lotka-Volterra competition model. Intrinsic growth rates and competitive coefficients are determined by the perceptive scales of particular species.

The intrinsic growth rate of a local population of species *x* on site *i* is equal to the average resource abundance \bar{r}_{ix} within the resource uptake region. To derive the competition coefficients, we introduce the concept of resource utilization distribution, which is the spatial pattern of individual resource consumption activity of a given species. It can be illustrated as a rectangular area above the resource uptake region with a width of S_x and a



Figure 2. Resource utilization distribution and competition function. **a** Resource utilization distribution can be represented by a rectangular region with area of unity above the resource uptake region. Length of horizontal and vertical sides correspond to perceptive scale S_x and consumptive burden on individual sites $1/S_x$, respectively. **b** Overlapping resource utilization distributions (white and black rectangles). With two individuals of species x and y on sites i and j at a distance of l, the competitive effect $a_{xy}(l)$ is equal to the consumptive burden of species y within the overlapping region of resource uptake regions $\omega_{xy}(l)/S_y$ (dark hatched region) times the consumption activity of species x on individual sites $1/S_{xy}$ yielding $a_{xy}(l) = \omega_{xy}(l)/(S_xS_y)$. Likewise $a_{yx}(l)$ is equal to the area of the total hatched region divided by S_y .

height of $1/S_{xr}$ corresponding to the consumptive burden on individual sites (Figure 2a). An individual of $S_1 = 1$, having a resource uptake region of only one site, has a very narrow and high resource utilization distribution. For species with larger perceptive ranges, the resource uptake region widens while the burden on individual sites decreases accordingly, resulting in wider and lower resource utilization distributions.

Individuals inhibit the reproduction of each other via competition, because their resource uptake regions overlap. The competition function $a_{xy}(l)$ expresses how much the population growth of species *x* on site *i* is inhibited by the presence of an individual of species *y* on site *i* + *l*, as a function of the distance *l* between them (Figure 2b). Competition is proportional to the overlap $\omega_{yx}(l)$ of the two resource uptake regions. It is also proportional to the consumptive burden of the inhibitor species on individual sites $1/S_y$ and the target species' likelihood of consuming resources from a given site within its resource uptake region at any given moment $1/S_x$. Also, we assume that species having larger body size and perceptive scale are able to

preempt resources from smaller-sized species, yielding:

$$a_{xy}(l) = \frac{\omega_{yx}(l)}{S_x S_y} \varepsilon \tag{3}$$

where $\varepsilon = (S_y/S_x)^{\alpha}$ if x > y; otherwise, $\varepsilon = 1$. α measures the strength of competitive advantage of large size due to resource preemption. The overall competitive burden on a local population p_{ix} is the sum of the competitive effects of all local populations within the potential competitive distance X + x - 2; for larger distances, $\omega_{yx}(l) = 0$.

Local populations interact via migration. Individuals leave a given site with rate c and settle in any of the L sites with equal probabilities. A migration rate of c = 0.1 enables moderate migration between local populations, without homogenizing the system. Ultimately, the dynamics of a local population is:

$$\frac{dp_{ix}}{dt} = p_{ix} \left(\bar{r}_{ix} - \sum_{l=-(X+x-2)}^{X+x-2} \sum_{y=1}^{X} a_{xy}(l) p_{i+l,y} \right) - cp_{ix} + \frac{c}{L} \sum_{j=1}^{L} p_{jx}$$
(4)

which is a cross-scale version of the familiar Lotka-Volterra dynamics.

To study population dynamics on different model landscapes, we solved this set of equations by numerical integration, using resource patterns $r_i^{\text{I}}, r_i^{\text{II}}$, and r_i^{III} . At t = 0, we had $p_{ix} = \sum_{i=1}^{L} r_i / (XL)$ for each species *x* and site *i*, assuring equal population densities of species and a total density in conformity with available resources. We ran simulations with dt = 0.01 until approaching an equilibrium density distribution at t = 2000, then recorded landscape-level average densities $d(S_x) = \sum_{i=1}^{L} p_{ix}/L$ of each species.

The model described here contains a number of simplifying assumptions. The model landscapes are characterized by a temporally constant resource distribution. Other important attributes of natural landscapes, such as fragmentation patterns, are ignored, and individuals have the potential to move to any point on the model landscape. All species are identical except for two attributes: perceptive scale and resource preemption ability. Population dynamics is under the control of competition; all other forms of species interactions are ignored. With all these simplifications, our aim was to study the influence of a few critical processes on important species characteristics and draw implications about body mass distributions. Possible effects of relaxing these simplifying assumptions will be addressed in the Discussion section.



Figure 3. Equilibrium species distributions. Vertical bars in the upper row show equilibrium species densities as a function of perceptive scales. $I(S_x)$ intensity functions are shown in the bottom row with gray resonance regions. Species densities and intensity functions are presented in three pairs, corresponding to the **a**, **b** homogeneous, **c**, **d** simple heterogeneous and **e**, **f** nested model landscapes. Vertical dashed lines indicate characteristic scales (σ and σ_1 , σ_2 , σ_3) of particular landscapes. Vertical dotted lines indicate positions of first resonance peaks.

RESULTS

From Eq. (1), it follows that small-scale variances of resource abundance, which do not alter large-scale averages, remain hidden for species with large perceptive scales. Although all species have access to the same resources, those with small perceptive scale exploit resource aggregations of comparable extent more efficiently by concentrating their feeding activity onto these sites. On local resource abundance peaks, high perceived resource abundance provides these fine-grained species a local competitive advantage over those with coarse-grained perception. On the other hand, large perceptive scale and body size implies increased competitive ability via resource preemption, independent of environmental heterogeneity. The set of coexisting species depends on the overall effect of these two opposite forces. Because perceived variance is a function of resource distribution, the outcome depends on the underlying landscape pattern.

We consider the homogeneous model landscape first (Figure 3a and b). From the viewpoint of individuals, there are no favorable or unfavorable sites, irrespective of their perceptive scales. The intrinsic growth rate is equal for all local populations at all sites; therefore the outcome of selection depends solely on other competitive relationships. The species of largest body size outcompetes all other species via resource preemption.

In a heterogeneous landscape, the experienced resource abundance \bar{r}_{ix} is no longer uniform, but varies with both spatial location and perceptive

scale. Individuals having larger intrinsic growth rates have a selective advantage; thus the ability to perceive favorable sites is crucial. Considering our second model landscape (Figure 3c and d), we see that the pattern intensity function I^{II} has a plateaulike region at small perceptive scales, starts to decline above $S_x = 32$, reaches a minimum at $S_x = 64$, and has resonance peaks with decreasing amplitudes at even higher S_x . This means that species with a given perception window are able to differentiate resource aggregates that are of compararable size, but not ones that are smaller. Given a square wave function with half-period σ , resonance peaks appear at $S_x = \sigma + h (2\sigma)$ $(h \in Z^+)$, as a result of the regular pattern. The performance of particular species depends on their ability to perceive and exploit local resource-abundant sites, requiring both a high degree of perceived landscape pattern intensity and good resource preemption capabilities. In our second model landscape, species that have relatively high resource preemption rank, but are still able to see favorable sites, outcompete others. Equilibrium species distribution has a single peak near $S_x = 32$, which corresponds to the scale σ = 32 of the underlying landscape pattern. The optimal perceptive scale is equal to the size of the resource aggregations; it also coincides with the point where the perceived intensity curve starts to decline.

Real landscapes have nested patterns. Our third model landscape has a nested resource pattern of three levels with one characteristic scale for each level: $\sigma_1 = 8$, $\sigma_2 = 32$, and $\sigma_3 = 128$. Species densities match this pattern, having peaks at

 $S_x = 8$, 32, 128 (Figure 3e). The coexistence of three species is the result of the peculiar spatial structure. In this case, species compete again in exploiting resource aggregations, but resource aggregations occur on three scales. Accordingly, perceived intensity can be broken down into three components, corresponding to heterogeneities on scales σ_1 , σ_2 , σ_3 as:

$$I^{III}(S_x) = I^{IIIa}(S_x) + I^{IIIb}(S_x) + I^{IIIc}(S_x)$$
(5)

 I^{IIIa} , I^{IIIb} and I^{IIIc} signify the performance of particular species in perceiving resource aggregations at the three scales (Figure 3f). They start to decline at different x, indicating that the perception of smaller-scale heterogeneities requires a small perceptive window; otherwise, the differences average out. Large species are superior in utilizing large-scale resources, but small ones with inferior resource preemption abilities can compensate by using small-scale resource aggregations. We have three nested levels within the landscape pattern, leading to the coexistence of three species. Their perceptive scales correspond to the points where intensity curves start to decline. These points are at $S_x = 8$, 32, and 128, corresponding to the characteristic scales of the landscape pattern.

Other small peaks in the density distribution are artifacts that originate from simplified model settings. Characteristic scales of model landscapes are powers of 2, because heterogeneities on such scales can be inserted neatly into each other to produce nested landscape patterns. In contrast, the perceptive scales of species are odd numbers; therefore a perfect match with landscape scales is impossible. The gap between these scales is filled by species x = 1, which uses small resource morsels, resulting in a small peak at $S_x = 1$. Furthermore, the species distribution for the third model landscape exhibits two resonance peaks at $S_x = 12$ and 48, which originate from resonance peaks of the intensity functions. These species ensure their survival by exploiting pairs of local resource aggregates; thus their existence is a consequence of the extreme regularity of the resource pattern. Simulations provided qualitatively the same results for $\alpha = 0.1$, 1, 10, and 100; coexistence was robust against changes in the magnitude of resource preemption capability.

DISCUSSION

These model results show that a nested landscape pattern and a corresponding resource distribution

enables the coexistence of species that perform the same ecological function on distinct scales. Given a nested landscape pattern, resource aggregations at different scales act as distinct resources, providing a set of scale niches. Although we restricted our simulations to a one-dimensional environment, we expect similar results for two dimensions and for fractal-like resource distributions. The dimensionality of the landscape in conjunction with the geometry of the area used by individuals, which varies with major taxonomic units, may be primary determinants of the scaling relationship between the spatial extent of resource aggregates and optimal perceptive scale (Witting 1995; Haskell and others 2002).

In our simulations we used a temporally constant landscape pattern, whereas real landscapes are also characterized by temporal changes. In spite of this simplification, our model also has implications for shifting mosaic landscapes, where temporal changes do not alter spatial scale pattern. Our model assumption was that population dynamics is dominated by local processes and local inhomogeneities. The scale of temporal changes expresses how ephemeral or persistent these inhomogeneities are. If landscape changes occur on short temporal scales, our assumption does not hold, because spatial heterogeneities average out on a very short time scale. On the other hand, if both the temporal and the spatial scale of environmental changes are very large, there is a conflict with our second modeling assumption-that animals have the potential to move to any point on the landscape. Organisms might also fail to interact with resources at the "appropriate" scales, if structural features of the landscape inhibit them, which often occurs as a result of anthropogenic impact (Roland and Taylor 1997). In these cases, our assumptions fail and other selection forces are expected to dominate, but for landscape changes of intermediate temporal and spatial scale we expect that our findings are valid.

The existence of scale niches suggests a mechanistic explanation for observed discontinuous body size distributions because of the allometric relationship between body size and perceptive scale. If distributions of various resources correlate with some common landscape features, difference scale inches might result in multimodal body size distributions within major taxonomic units, even if species consume different resources. Dissimilar landscapes have different sets of scale niches, with corresponding perceptive scale and body size distributions. Nevertheless, the evolution of a trait such as body size, which is subject to many historical or ecological constraints, is not likely to be explained by a single mechanism. Other evolutionary and ecological processes, such as trophic relationships, may also play a role in determining body size (Vezina 1985; Carpenter and Kitchell 1993; Siemann and Brown 1999; Cumming and Havlicek 2002). Ritchie and Olff (1999) emphasized the importance of spatial scaling laws in explaining both the size and diversity patterns of organisms.

The reorganization capabilities of ecosystems may be influenced by such functional redundancy across scales because ecological resilience depends on the distribution of functional groups both within and across scales (Peterson and others 1998). Although our model is in agreement with this view, the issue of ecosystem resilience requires further research. Selection constraints, imposed by scale attributes of landscape patterns also raise other biological conservation issues. Scale niche shifts due to landscape transformations may result in a corresponding change in species composition (Morton 1990). The mass extinction of megaherbivores in North America during the Pleistocene was related to the landscape transformation ability of invading human populations, apart from hunting pressure (Webb 1984; Lambert and Holling 1998). Accordingly, empirical studies have shown that both invasive and endangered species are located at the edge of body mass aggregations (Allen and others 1999; Sendzimir and others 2003).

Environmental changes on several scales require appropriate biological adaptations (Wiens 1989). The fact that numerous large species are now endangered implies that anthropogenic disturbances primarily threaten species that are susceptible to changes in large-scale landscape features. Natural environmental perturbations due to ecological, climatic, or geological processes show an inverse relationship between frequency and amplitude; thus large-scale perturbations occur only rarely or slowly (O'Neill and others 1986). In contrast, anthropogenic landscape transformations affect large areas in a relatively short time, presenting novel challenges for conservation biology.

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