

Ecological neighborhoods: scaling environmental patterns

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In this paper we review, develop, and differentiate among concepts associated with environmental patterning (patch, division, and heterogeneity), spatial and temporal scales of ecological processes (ecological neighborhoods), and responses of organisms to environmental patterning (relative patch size, relative patch duration, relative patch isolation, and grain response). We generalize the concept of ecological neighborhoods to represent regions of activity or influence during periods of time appropriate to particular ecological processes. Therefore, there is no single ecological neighborhood for any given organism, but rather a number of neighborhoods, each appropriate to different processes. Neighborhood sizes can be estimated by examining the cumulative distribution of activity or influence of an organism as a function of increasingly large spatial units. The spatial and temporal dimensions of neighborhoods provide the scales necessary for assessing environmental patterning relative to particular ecological processes for a given species. Consistent application of the neighborhood concept will assist in the choice of appropriate study units, comparisons among different studies, and comparisons between empirical studies and theoretical postulates.

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Introduction

Environmental patterning refers to the non-uniform, spatial and temporal distribution of resources and abiotic conditions that influence species or species interactions. Such patterning is pervasive in nature and is known or hypothesized to affect many ecological processes and phenomena, including population dynamics, life histories, dispersal, foraging behavior, patterns of natural selection, coexistence of species, predation, and species diversity (e.g. Huffaker 1958, Southwood 1962, Levin and Paine 1974, May 1974, Roff 1974, Wilbur et al. 1974, Levin 1976, Chesson 1978, Pleasants and Zimmerman 1979, Shorrocks et al. 1979, Denno et al. 1980, Hassell 1980, Wilson 1980, den Boer 1981, Paine and Levin 1981, Kareiva 1982, Spence 1983). Therefore, the

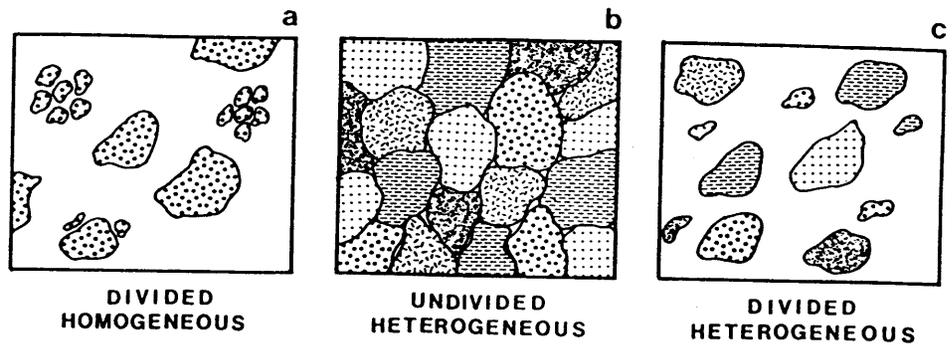
study of environmental patterning and how organisms respond to it has become a central focus of current ecological research.

However, there are no general procedures and criteria for determining how organisms respond to or are affected by environmental patterning. Convenient but arbitrary spatial and temporal study units may be inappropriate for the processes being studied (see discussion by: Brown and Kodric-Brown 1977, Connell and Sousa 1983, Connor et al. 1983, Cunningham 1986), and conclusions appropriate to one scale of environmental or population patterning may be inappropriately transferred to another scale (e.g. Price 1980). Without a reasonable means of scaling, it is difficult to compare results from the same species in different environments, from different species in the same environment, or be-

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Fig. 1. Examples of combinations of divided and heterogeneous environments. Different patch types are denoted by different patterns of shading. Notice the variation in patch size, and the existence of patches of patches.



tween theoretical postulates and empirical results. Therefore, a precise and unified approach to the study of patterning and responses to patterning is needed.

In this paper we first discuss concepts associated with environmental patterning: patch and environmental division/heterogeneity (Wiens 1976, Shorrocks et al. 1979, Gould and Stinner 1984). Second, we develop a generalized concept of ecological neighborhoods (Wright 1943, 1946, Southwood 1977, Antonovics and Levin 1980). Ecological neighborhoods then provide a mechanism for scaling both spatial and temporal patterns of the environment relative to organisms. Next, we develop explicit procedures and criteria for implementing the concept of ecological neighborhoods. Finally, we discuss why scaling is necessary in ecological studies. Our intent is to encourage the use of more explicit criteria for defining and reporting on environmental patterning and the responses of organisms to it.

Environmental patterning

The study of environmental patterning involves descriptions of the spatial distributions of both resources and abiotic conditions. When environmental variables are discontinuous among arbitrarily chosen sampling units, environments are said to consist of patches. A patch is defined as a discontinuity in environmental character states where the discontinuity matters to the organism (Wiens 1976), as a "bounded, connected discontinuity in a homogeneous reference background" (Levin and Paine 1974), or as any place in the environment where the abundance of either resources or organisms is high or low relative to its surroundings (Roughgarden 1977). These definitions can be implemented by using any of a variety of statistical procedures (see Pielou 1969, Ripley 1981).

We distinguish two qualitatively different kinds of patterning: division and heterogeneity (Shorrocks et al. 1979, Gould and Stinner 1984). Division involves the separation of patches by regions of relatively unsuitable environmental conditions (Fig. 1a,c), where suitability is defined in terms of the fitness (or components of fit-

ness) that an organism would experience within a patch (Southwood 1977). Heterogeneity involves the existence of two or more qualitatively different patch types (Fig. 1b,c) that may or may not differ in suitability. Environments could be divided and homogeneous (Fig. 1a), heterogeneous but not divided (Fig. 1b), or both divided and heterogeneous (Fig. 1c). In a divided environment, the interpatch region could represent environments where the fitness of an organism would be zero (Southwood 1977), such as marine environments for terrestrial insects or all plants except flowering yuccas for yucca moths. Alternatively, the interpatch region could represent environments in which fitness is relatively low, but non-zero. Each type of patterning exists as a continuum, with variation from continuous to divided environments, and from homogeneous to heterogeneous environments.

Patchy environments increase the difficulty of making appropriate choices of temporal and spatial scale for study units. The distribution of organisms and patterns of resources may not reflect an organism's use of the environment. Simply identifying the existence of patchiness does not mean that the patchiness is important for a particular process. Next, environments can simultaneously exhibit patchiness at a number of different spatial scales, from millimeters to kilometers (Krebs 1978). However, a simple description of patch structure of either an organism or its environment would not indicate which spatial scale is appropriate for the study of a given process for a given organism (Connor et al. 1983, Heads and Lawton 1983). Finally, different species may treat patch sizes differently. A simple description of environmental or population patch structure provides no biologically meaningful way of comparing patches among different organisms (Southwood 1977). Comparisons must be based on the responses of organisms.

A general concept of ecological neighborhoods

Therefore, we need a mechanism for determining the scale at which experiments or observations should be

made, and this scale will in turn measure patch size, patch duration, patch isolation and use of heterogeneous patches relative to organisms. The concept of ecological neighborhoods is appropriate for this task. Here we expand and generalize neighborhood concepts developed by Wright (1943, 1946), Southwood (1977) and Antonovics and Levin (1980) for scaling genetic or ecological processes. Our generalized version of the concept of ecological neighborhoods refines earlier uses to make it applicable to any ecological process and to both mobile and sessile organisms.

We define ecological neighborhoods by three properties: an ecological process, a time scale appropriate to that process, and an organism's activity or influence during that time period. The ecological neighborhood of an organism for a given ecological process is the region within which that organism is active or has some influence during the appropriate period of time. This concept of neighborhood could apply to any ecological process, such as population growth, predator-prey interactions, competition, foraging behavior, or territorial defense. The choice of an ecological process will define an appropriate time scale over which to measure neighborhood size. As with genetic neighborhoods, it may be convenient to refer to either the physical size of the neighborhood or the number of individuals within the neighborhood.

For relatively mobile organisms, the movement of individuals will usually define the neighborhood (Dobzhansky and Wright 1943, Lloyd 1967, Koepl et al. 1975, Jumars 1976, Ford and Krumme 1979). For sessile organisms, neighborhoods will frequently be restricted to the immediate vicinity of a single individual, depending upon the precise mechanism of resource utilization or interference with other individuals (Connell 1961, Mack and Harper 1977, Antonovics and Levin 1980). However, in some cases regions of influence can extend well beyond individuals whether they are mobile or sessile. This will occur when 1) consumable resources are mobile with respect to an organism such as for sit-and-wait predators or filter feeding invertebrates (e.g. Buss and Jackson 1981), 2) an organism produces some potentially deleterious by-product that is carried in the air or water (e.g. allelopathy) (Pratt 1966, Lewis 1986), and 3) an organism attracts its consumers or its mutualistic foragers from a wide region (e.g. Manasse and Howe 1983).

Responses to environmental patterning

Relative patch size, isolation, and duration

Ecological neighborhoods provide appropriate scales for measuring the relative size, isolation, and duration

of patches in a patterned environment. Relative patch size is simply the ratio of patch size to neighborhood size. Patches of a given size are relatively small if a neighborhood encompasses a number of them, and relatively large if a neighborhood encompasses only part of one patch (see Southwood 1977). In a divided environment, patches are separated from each other. The size of the region separating patches may be just as important as the size of patches themselves (Southwood 1977). Therefore, it is also appropriate to scale interpatch distances by neighborhood sizes, leading to the concept of relative patch isolation. For example, Southwood's (1977) definition of an isolated habitat includes the idea that interpatch distance must be large relative to an organism's migratory range, "the area over which it can move when it is not reproducing".

Temporal patterning of environments is also important, because patch duration (= temporal persistence) may range from seconds to millennia (Levin and Paine 1974, Paine and Levin 1981). The basis for comparing patch duration is the time period appropriate to a given neighborhood (see Connell and Sousa 1983). Relative patch duration provides an assessment of whether patches are permanent or ephemeral with respect to a given process and organism (Southwood 1977, Connell and Sousa 1983). As with patch size, any given patch could be relatively permanent or ephemeral simultaneously, depending upon the neighborhoods and organisms being considered.

The interaction between relative patch size and relative patch duration may be complex. Temporal environmental patterning may affect the mobility or life history of organisms, and these will in turn affect neighborhood size. If resources in a given patch are insufficient for the completion of an entire life history stage, then individual organisms must disperse from one patch to another as patches are depleted (see Chew 1977). An alternative response to ephemeral resources is the evolutionary modification of either dispersal behavior or duration of life history stages to match the temporal availability of resources (e.g. Taylor 1980a,b).

Grain: responses to environmental heterogeneity

For heterogeneous patches, utilization of the different patch types can be random, in proportion to their availability, or non-random, with some patch types used more frequently than their relative availability and others less frequently. These represent fine and coarse grain responses, respectively. Although the term grain has been used in other contexts (MacArthur and Levins 1964, Levins 1968), it is most useful as a concept for the response of an organism to environmental heterogeneity. As with relative patch size and duration, grain is relative to a given process and period of time. With this definition, grain is not a property of an environment; there are not fine and coarse grained environments.

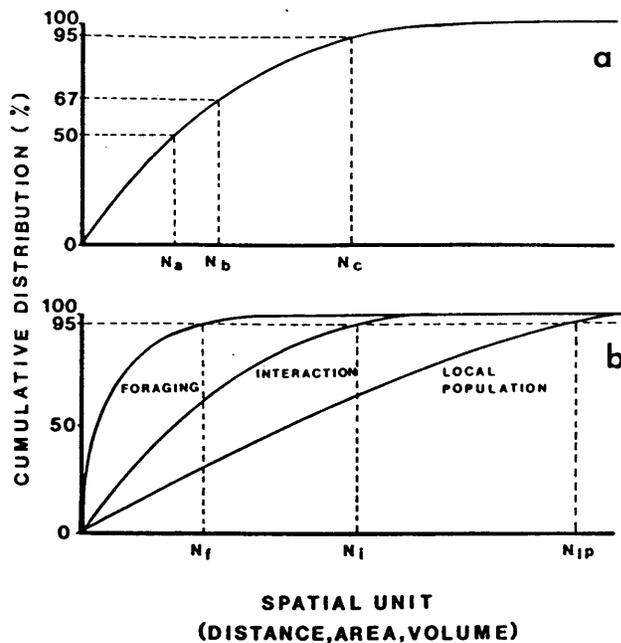


Fig. 2. Hypothetical examples of the relationship between cumulative distribution of movement or influence against spatial unit. Horizontal dotted lines at arbitrary points on the cumulative distribution indicate different neighborhood sizes for different decision criteria (Fig. 2a). Each curve in Fig. 2b represents a cumulative distribution with an associated neighborhood size for a different ecological process, using a decision criterion of 95%.

only fine and coarse grained responses by organisms to environmental heterogeneity.

Neighborhoods, relative patch sizes, and grain are also potentially interrelated. If patches are large relative to a given neighborhood, grain response to those patches must be coarse. If patches are relatively small, however, grain response could be either fine or coarse. More complex situations will arise when patches of different quality also differ in size or duration.

Estimating neighborhood size

There are two problems involved in measuring neighborhoods. The first is to develop procedures for measuring the distribution of activity or influence among sampling units. The second is to develop criteria for determining the boundaries of a neighborhood. These criteria will be arbitrary, but they should be explicit. The procedures needed to measure the distribution of activity or influence will depend on the kinds of neighborhoods and organisms being studied.

For neighborhoods such as local reproductive population neighborhoods that involve relatively long time pe-

riods, the most appropriate indicator of activity may be a measure of net movement of individuals (or their gametes or progeny) among sampling units during the period of time appropriate to the neighborhood. There are two general sets of procedures for measuring net movements. One is the direct measurement of dispersal distances, using a mark-release-recapture technique at a number of sampling sites to determine the cumulative frequency distribution of dispersal distances (Dobzhansky and Wright 1943). The other is to measure the distribution of locations where an organism occurs throughout an appropriate period of time (Koepl et al. 1975, Ford and Krumme 1979). For some kinds of organisms and neighborhoods, assessment of influence will not be a function of the movement of that organism. For example, for interaction neighborhoods in sessile organisms, the regions from which resources are obtained or depleted, or the regions from which predators or mutualistic foragers are attracted by neighboring individuals must be measured (e.g. Buss and Jackson 1981, Manasse and Howe 1983).

Given a distribution of activity or influence, neighborhood size is then defined by the distance, area, or volume representing some arbitrary but explicit point on the distribution (Fig. 2a). If the concept of neighborhood is to be useful, the decision criterion must be consistent, explicit and reasonable. For population dynamics we want to identify a neighborhood where most of the population growth is due to in situ reproduction rather than due to immigration (Connor et al. 1983). For interaction groups we would want to identify the neighborhood from which most potentially limiting resources are obtained (Antonovics and Levin 1980). It is not clear a priori whether a criterion of 50%, 67% or 95% is reasonable (Koepl et al. 1975). Moreover, the arbitrary nature of the decision criterion is clearly shown by comparing the importance of dispersal in a genetic and ecological context. The movement of a very small number of individuals can maintain genetic uniformity among populations (Roughgarden 1979:203), but the same amount of dispersal may have little effect on population dynamics. Until there is an accumulation of studies of neighborhoods, it is not so important that the criterion be common to all workers, but it is imperative that the criterion be explicit. Fig. 2b provides an example of how a decision criterion of 95% would be applied to define three different neighborhoods for a single organism.

Why scaling is necessary

Three major problems arise if the size of study units is arbitrary rather than based upon a scale appropriate to organisms and questions. First, it will be difficult or impossible to make comparisons of experimental or observational results among different species in either the same or different systems, because arbitrarily chosen

study units may represent different scales (= neighborhood types) for each species. For example, in a study of the establishment, extinction, and dynamics of aphids on fireweed, Addicott (1978a) assumed that aphids on individual ramets represented local populations for each of four species of aphids. This arbitrary assumption seemed reasonable based upon the mobility of apterous aphids, population densities of aphids on individual ramets, and the work of others (Hughes 1963, Sanders and Knight 1968). However, we now know that this assumption was appropriate for *Aphis varians* but not for *Macrosiphum valerianae*; there is little or no movement of apterous *A. varians* from ramet to ramet within a clone of fireweed, whereas *M. valerianae* are relatively mobile (Antolin and Addicott, unpubl.). Therefore, analysis of data from individual ramets of fireweed relates to different levels of population structure in the two species. Comparisons of species with distinctly different life histories will be even more difficult. For example, it will be difficult to compare the responses to patterned environments for organisms as different as aphids (e.g. Addicott 1979) and birds (e.g. Rotenberry and Wiens 1980) unless we can tell whether or not each has been studied at the same relative scale.

The second problem arising from an arbitrary choice of spatial units is that a given patch size need not necessarily correspond to the particular ecological neighborhood appropriate for examining a given ecological model (see Connor et al. 1983, Heads and Lawton 1983). Therefore, it will be difficult to relate field experiments or observations to particular theoretical models or conceptual postulates, and conclusions about those models could be flawed. This would clearly be the case in the fireweed system, where individual ramets do not represent local population neighborhoods for *M. valerianae*. Data on *M. valerianae* on individual ramets should not be related to models of the dynamics of patch occupation that are based upon local populations as the unit of observation. This does not mean that it is necessarily inappropriate to study systems at arbitrary and convenient spatial scales. However, it may be inappropriate to compare data sets among different systems or with conceptual models. Since such comparisons are an essential part of our science (Connell 1983, Schoener 1983), it is important that study units be based upon appropriate and clearly identified scales.

The third problem is that different processes in the same system may occur at different scales, and therefore it may not be sufficient to examine a particular system at only one spatial or temporal scale. For example, in the aphid-fireweed system there are a number of processes that affect the dynamics of local populations of aphids, but these processes occur at a variety of scales. Competition neighborhoods can be as small as the immediate vicinity of an individual aphid for behavioral interactions (e.g. Whitham 1979), individual ramets for competition based upon plant resources, or clones of fireweed for competition for the services of ants (Addi-

cott 1978b). Predation neighborhoods can be as small as single ramets for the predaceous mites of aphids, one or more clones of fireweed for insect predators or parasitoids, or all fireweed ramets in whole drainages for avian predators of aphids. The variety of neighborhood sizes complicates the study of organisms in patterned environments, because it is extremely difficult to examine processes simultaneously that may be occurring at two or more spatial or temporal scales. However, an adequate understanding of the dynamics or behavior of a system may demand just that.

Discussion

In this paper we have made three main points. First, we believe that it is essential to distinguish between three conceptually distinct but biologically interrelated concepts: 1) the distribution of environmental variables as represented by temporal and spatial patterns; 2) the area of activity or influence of organisms during appropriate periods of time that define what we call ecological neighborhoods; 3) the use of ecological neighborhoods to scale environmental patterning, thereby allowing assessment of relative patch size, relative patch isolation, relative patch duration, and relative utilization of heterogeneous patches (grain response).

Second, the concept of ecological neighborhoods needs to be general; there should not be just one kind of process or a limited number of time or dispersal distances that should be used to scale ecological processes. Instead, each process and interaction should be examined to determine an appropriate neighborhood, defined by movement or influence during an appropriate period of time. Thus, a single, general concept of ecological neighborhoods can be applied at a variety of levels, rather than having a series of apparently unrelated concepts and terms such as ambit (Lloyd 1967, Jumars 1976), home range (Koepl et al. 1975), territory, local population (Wright 1946), etc. Therefore, we have generalized the concepts of scaling and ecological neighborhoods, as developed by Southwood (1977) and Antonovics and Levin (1980).

Third, scaling of ecological observations is extremely important. Ecological neighborhoods provide a basis for scaling the patterning of environments relative to organisms, which in turn provides the basis for comparing species in the same system, comparing processes among organisms in different systems, making appropriate comparisons between field studies and theoretical models, and for designing field studies of population interactions at one or more appropriate scales.

Implementing the neighborhood concept by measuring neighborhood sizes and using them to scale environmental patterning will be hindered by at least five major problems. First, there will continue to be conflict between the ease of choosing study units to correspond to patch sizes and the fact that ecological neighborhoods do not necessarily correspond to patches. Similarly, the

scale at which a study can be conveniently conducted may not correspond very closely to a neighborhood that should be ultimately of interest to the investigator. Third, as has been the case with genetic neighborhoods, it will be difficult to actually obtain the data required to assess neighborhood sizes. Fourth, the criteria for establishing neighborhood size are necessarily arbitrary, and there is as yet no consensus on rationale for choosing one decision criterion over another. Finally, organisms are affected by a variety of processes, each of which may have a different neighborhood size associated with it.

Despite these practical difficulties, it is imperative for ecologists to begin to report the scale(s) at which their observations and experiments are made. This could involve a detailed analysis of neighborhood sizes relative to the sizes of study units and patches, or it could simply involve reporting qualitative impressions of the natural history of the study organism to justify the use of a particular study unit. However, the future development of ecology will be hindered not by the absence of appropriate concepts and techniques for scaling environmental patterning, but rather by the failure to recognize the overriding importance of scaling for facilitating comparisons between studies and comparisons between theoretical postulates and empirical work.

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