

Ecological Scale

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A HIERARCHICAL VIEW OF HABITAT AND ITS RELATIONSHIP TO SPECIES ABUNDANCE

Jurek Kolasa and Nigel Waltho

Ecologists often study communities by sampling and analyzing richness and abundance of species grouped by evolutionary taxonomy or appearance. Abundances of such species usually show two general patterns (figure 4.1). One relates to the shape of rank-abundance curves and the other to the relationship between the ecological range and abundance of species. The rank-abundance curves are generally concave or hollow in shape when plotted on the arithmetic scale (Magurran 1988; Tokeshi 1993). Such curves have been shown to fit a variety of related statistical distributions (May 1975; Sugihara 1980; Magurran 1988; Tokeshi 1993) and occasionally to have mysterious properties such as the canonical lognormal form (Preston 1948).

Niche-oriented models (MacArthur 1957; Whittaker 1965; Sugihara 1980; Tokeshi 1990) concentrate on resource subdivision, but they are weak on other ecological factors known to affect abundances. The resource subdivision approach itself has serious conceptual inconsistencies when it is cast in terms of niche. For example, niche dimensions describe different resource types, but they cannot capture the resource amounts (if they did, then the niche of a species would change dramatically from year to year depending on resource supply). In addition, niche dimensions have no spatial component, which may be crucial to species density (Leibold 1995; but see Silvert 1994). The focus of much previous research on fitting particular distributions to rank-abundance data has been a limited research strategy. Few sound ecological reasons have been offered (MacArthur 1957; Engen 1978; Frontier 1985) to support the view that the data should show any specific fit at all

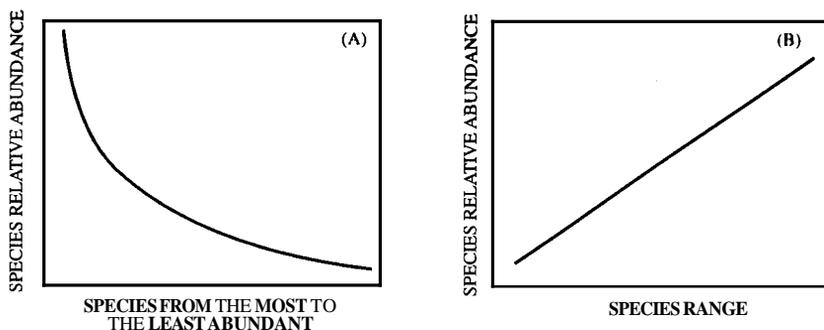


FIGURE 4.1

Species abundance patterns. (A) A generic pattern of species abundance distribution from a local or regional collection. (B) A typical relationship between species abundance and size of geographical range (as measured by area, number of sites, or latitude).

(Tokeshi 1993). When such reasons were provided (Sugihara 1980), the tests were faulty. For example, Nee et al. (1991) used a geographical distribution to test community level fit of data to the sequential breakage model whose ecological motivation is local or at best regional. However, when ecologists proposed ecological mechanisms under which species would exhibit regular patterns in distribution of abundances, they were successful in predicting quantitative trends (Brown 1984; Hughes 1986) and qualitative characteristics, such as the bimodal distribution of abundances (Hanski 1982), but not in predicting specific fits. The mechanism-focused approach is a better route to pattern detection and interpretation.

Ecological range and abundance have often been found to be positively linked (Hanski 1982; Bock and Ricklefs 1983; Brown 1984; Kolasa 1989; Gaston and Lawton 1990; Maurer 1990; Collins and Glenn 1991; Lawton et al. 1994). This means that habitat generalists are locally more abundant than habitat specialists (Kolasa and Drake 1997). However, sometimes researchers do not state clearly whether they mean a total count of a species in a collection or its density only in the habitats it occupies, or its density over the area of interest, including empty sites. The total observed abundance of habitat generalists, at the same density, will almost inevitably be higher because they occupy more habitat space. However, it is not obvious why the density of a habitat generalist should be higher than that of a specialist. It is

thus useful to make a distinction between abundance and density (often termed local abundance), and we will interpret the pattern with a **focus** only on density. Gaston's (1994) considerations of rarity and scale are instructive in this context.

According to Hanski et al. (1993), there are three explanations of the range–abundance relationship. First, the sampling model attributes the relationship to the underestimation of distribution of rare species. This model is essentially correct in that it has a strong rationale and a detectable effect. It may constitute an adequate explanation in some situations in which the sampling methodology is exceptionally weak, but it is insufficient in other situations (see later). Second, the ecological specialization model (Brown 1984) assumes that species density follows a bell-shaped form over its geographical range. If the form is kept constant, the smaller ranges will produce lower peaks (corresponding to densities) in the respective curves (figure 4.2a). The area under the curve, which represents total abundance, will also be smaller.

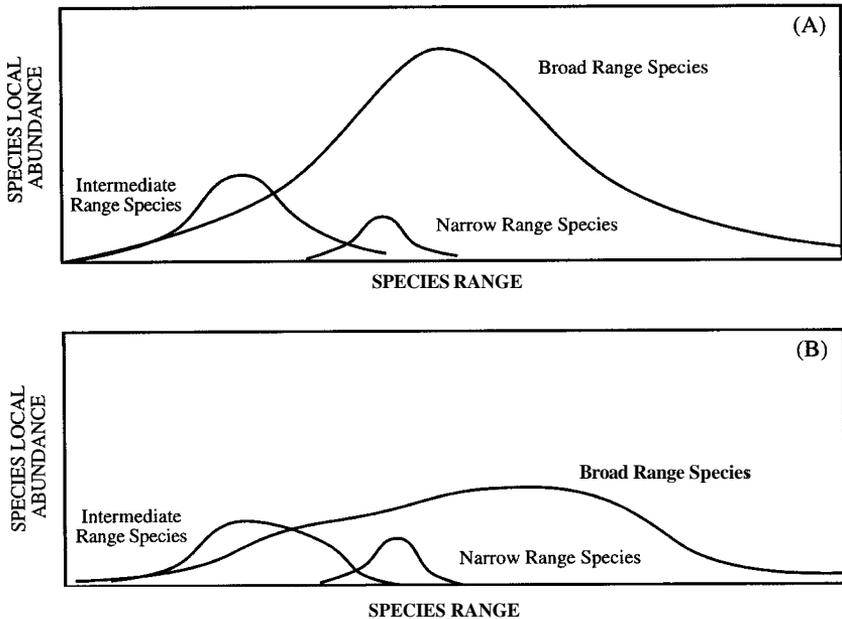


FIGURE 4.2

Species density over a geographical range. (A) According to Brown's model of specialization. (B) A more realistic form with hypothetical plateaus.

For this model to work, one must assume the same general shape for the bell curve for most species under consideration. If one sampled a pool of similar bell-shaped curves, those with broader bases would, on average, have higher peaks and higher mean densities. The assumption of curve similarity lacks an ecological justification. In contrast, curves may display a variety of shapes, with distinct plateau regions where densities would neither increase nor decrease significantly (see figure 4.2b). Furthermore, actual data do not show that widespread species have enormous densities in the center of their geographical range. The value of the Brown model lies in its emphasis on species properties (see later). Third, the pattern of abundance could be produced by metapopulation dynamics (Hanski 1982; Hanski et al. 1993). Occupancy of separate patches is linked to mean population density via probabilities of immigration and extinction. A net result is that species of limited distribution also maintain low population density.

This chapter reconciles the above propositions in one scale-independent model. We explore a conceptual approach to the problem of community organization. This approach appears (1) to solve the problem of explanation of species abundance and related patterns, and (2) to emphasize integration of previously unrelated phenomena and processes. The approach builds on previous attempts to deal with these patterns. Specifically, it combines the attributes of and differentiation among species, as well as the attributes and structure of the habitat in which they live. In other words, it combines the perspectives of classical community ecology, island biogeography, patch dynamics, metacommunity, and landscape ecology. The rest of the chapter discusses this specific approach expressed in the form of a conceptual model. Although we elaborate the foundations of the model in greater detail than in previous papers, we also emphasize the operational aspects. In particular, we examine various field and analytical situations that ecologists are likely to encounter, and we provide suggestions and examples relevant to implementing the model.

Habitat-Based Model: General Approach

Unlike the niche-apportionment models, the habitat-based model (HBM) treats species and their habitat as separate variables. This approach is designed to be consistent with the logic of evolution, in which the interaction of the phenotypic pool of individuals with the environment determines their success in the next generation. In the HBM, by

analogy, the anticipated patterns of abundance are viewed as the product of the interaction between species attributes and habitat attributes such that

$$\text{Abundance}_i = k (\text{specialization}_i \times \text{habitat}_i)$$

where k is a species–habitat adjustment factor that may take into account such factors as habitat quality. Specifically, the habitat of species i is expressed as a fraction of the parameter range with which the entire set of species interacts. Specialization is expressed as a ratio of ecological range of species i to that of the broadest species in the habitat unit under investigation, and it is calculated in units suitable for a particular system.

The model uses assumptions about (1) species attributes, (2) habitat attributes, and (3) the relation between species and habitat. It incorporates only those assumptions that apply universally to all species and all habitats, making it a general model. These assumptions are discussed next.

Assumptions: Species

Assumptions concerning species attributes relevant to the model interpretation apply only to habitats or regions whose species show one of the patterns described in the introduction. The assumptions are (1) that species differ in their ecological requirements and, thus, there will be some species with narrow and others with broad requirements (specialists and generalists, respectively) and (2) that any habitat may host a set of species representing a range of requirements from narrow to broad. Explanation of the assumptions about species will help avoid ambiguities and misunderstandings associated with textbook stereotypes. Different ecological requirements can imply many things, such as tolerance limits, resource needs, and conditions for successful reproduction and dispersal. For example, presence of certain pollinators may have a critical impact on the performance of a species in a particular habitat, and absence of wind may make patch recolonization difficult. Such a species may end up in few patches and will thus be considered a habitat specialist. Indeed, the terms *specialist* and *generalist* have a variety of meanings in ecology. The meaning here is general but precise: a specialist is a species restricted to a small volume of the multidimensional habitat space. In contrast, a generalist is a species that is not so restricted. Note that a species is evaluated by its relation

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to the habitat, and it is defined as specialist or generalist relative to other species in the community, which jointly define the multidimensional habitat space (see the next section on habitat). In a different habitat, classification might reverse, although this is not very likely. For these distinctions to be meaningful, one should evaluate species at a habitat scale at which species attributes are likely to make a difference in their performance as populations. At very small scales, immigration or emigration of individuals may cloud the relationships. Because abundance is a function of both habitat and species attributes (table 4.1), this flexibility of specialization concept is a strength rather than a liability.

The concept of specialization used here implies little about ecological efficiency. First, we wish to clarify the meaning in which the term is used. Specialization comes in two logically indistinguishable extremes: evolutionary specialization (genetically constrained) and ecological specialization (constrained only by immediately acting factors). All transitions between the two types are possible. Only the latter type responds dynamically to the change of conditions at a short time scale; this is the one of interest for the model we present. Although specialists may be more or less efficient in using accessible resources, many ecologists believe that specialists are generally more efficient. This advantage does not translate well into abundance patterns in the context of the proposed model, because consequences of habitat fragmentation

TABLE 4.1
Details of interpretation of species attributes

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1. A species has ecological characteristics that can be expressed in an n -dimensional hyperspace, and when so expressed they will form a species ecological hypervolume.
 2. These characteristics include variables permitting the species to exist and variables describing species impact on other components of the environment and other individuals of the same species.
 3. Only those variables that define a species' ability to exist in an environment (thus, a portion of the hypervolume) are considered in connection with the habitat concept and approximate (but are not equivalent to) the concept of niche (the disclaimer is necessary primarily because of the lack of precise niche definition). Amount of resource is not a component of this hypervolume. If it were, the assessment of the habitat structure would be impossible. If quantity of resource were a part of a species hyperspace, then niche volume would be determined almost entirely by the number of individuals, N thus rendering the concept of the niche useless, no matter how imprecise it is. The amount of resource determines N of a species but not its ecological characteristics.
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and attendant size reduction (figure 4.3) are much greater (Kolasa and Strayer 1988). However, greater efficiency of resource utilization may make a difference between survival and extinction in a fragmented habitat.

We avoid using *niche* for describing ecological properties of species despite the fact that the concepts presented here have some affinity to the concept of the niche. There are many different interpretations of niche. Silvert (1994) and Leibold (1995) clarified important aspects of the niche concept, but until their ideas are more broadly accepted and supersede a plethora of earlier uses, the term will keep generating confusion. We limit ourselves to citing Silvert (1994) who stated that niche can be thought of as a generalization of range. Silvert views the niche as a collection of points in a multidimensional space where the species

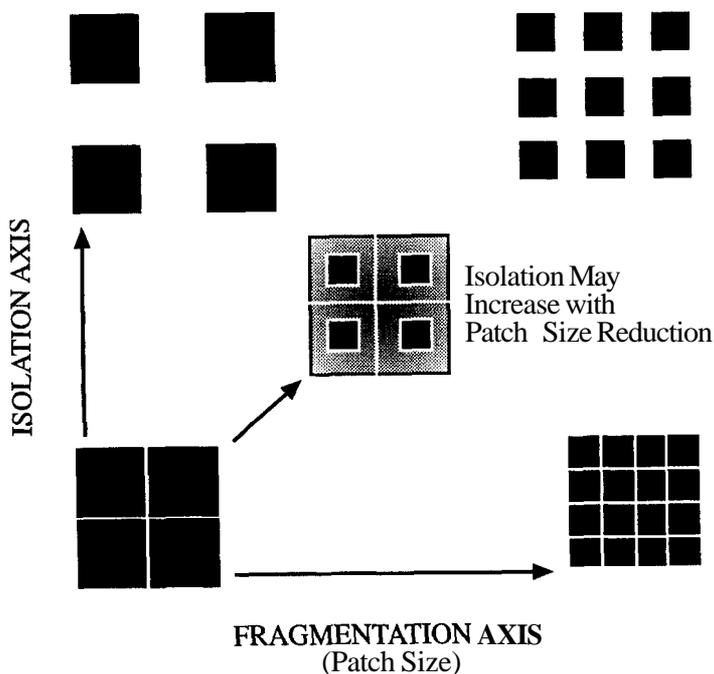


FIGURE 4.3

Fragmentation, isolation, and habitat size reduction. In most cases, increasing fragmentation is likely to correlate with the reduction of habitat size, although this may occur at the expense of the total habitat available or through emergence of interpatch barriers.

is observed. The difference between our use of niche and that of Silvert's is that observation of distribution is only a subset of species properties already defined by the available habitat template (see later).

Some species appear as specialists because of evolutionary constraints, whereas others may be products of novel or unusual circumstances. For example, many species requiring oligotrophic and cold lakes are currently habitat specialists, even though they may have appeared as habitat generalists 20,000 years ago. Some species may appear as specialists because of one particular limitation such as diet, whereas others may appear so because of a synergistic effect of several milder limitations. The reasons for the limitation may also vary greatly from immediate ecological factors such as trampling or seedling grazing to evolutionary constraints such as the inability by most mammals to chase insects in the air. For example, Tilman's (1982) resource ratio hypothesis illustrates how presence of competitors may limit the range and number of species with higher threshold levels of nutrient concentrations. Hanski's (1982; Hanski et al. 1993) metapopulation models call attention to dispersal abilities and their consequences. Natural history provides hundreds of other examples for different types of habitat limitation. Predation, ontogenetic shifts in habitat requirements, habitat connectivity (Milne 1992), magnitude of rescue effects (Stevens 1989), and heterogeneity of energy supply at regional scale (Wright et al. 1993a) all address one or several mechanisms limiting species in habitat space. These limitations may be fairly permanent or dynamic and variable. In all these cases, the HBM is concerned only with the actual status of a species in the community under consideration. This status affects a species' current performance, which, in turn, is subject to predictive deductions by the model.

Assumptions: Habitat

Before model assumptions can be presented, we need to clarify what we mean by *habitat*. Despite a long history of the habitat concept (Whittaker et al. 1973; Rejmanek and Jenik 1975; Wiens 1984; Addicott et al. 1987; McCoy and Bell 1991), the meaning and usage of the term are far from clear. This lack of clarity is intricately linked to the niche concept, which also has several inconsistent interpretations (Hutchinson 1957; Whittaker et al. 1973; Pianka 1976; Haefner 1980; Giller 1984; Herbold and Moyle 1986; see table 4.2 for several definitions and brief comments).

Species attributes and habitat attributes are two different things. Al-

though they differ, they cannot be separated fully; they co-define each other as a key and lock are co-defined (in a hypothetical world without locks, the concept of key would have no meaning). We base further discussion on the following assumptions and definitions, some of which may sound trivial but are actually necessary for the completeness of the argument:

1. The physical world has an infinite number of descriptive dimensions.
2. Some of these dimensions form a subset relevant to ecology. This subset can be treated as, and used to characterize, an environmental template.
3. The subset is spatially and temporarily heterogeneous: values in each dimension may vary from place to place and time to time.
4. A combination of dimensions and a subset of dimension values (i.e., a portion of the template) that interact with a species, constitute the species habitat or multidimensional habitat space.
5. The portion of the template that interacts with a species is determined by a subset of species attributes. For example, lakes differ in phosphorus (P) concentration, and if a species requires a particular concentration of P (a dimension), interaction is likely to occur. (See table 4.1 for further explanation and comments on the concept of habitat.)
6. Portions of the physical environment match or fail to match the “niche” dimension values because they vary quantitatively (e.g., the amounts of resources: no resource—no match, correct concentration—perfect match).
7. Arrangement of those portions in space and time is habitat structure (McCoy and Bell 1991).
8. The totality of all species habitat spaces is the community habitat space.

A more precise definition of species attributes helps in identifying habitat structure. Consider the case of *Myrmecophaga tridactyla* (ant-eater). Let us use only a few dimensions, such as the habitat elevation and diet spectrum. *M. tridactyla* cannot feed under conditions of prolonged flooding because it normally requires high abundance of insects such as ants and termites. These dimensions constitute a subset of ecological attributes of *M. tridactyla* and roughly correspond to some interpretations of the niche. Other, nonniche attributes of *M. tridactyla* may include its reproductive strategy, destructive impact on termite nests (but see Leibold 1995), or intelligence. South American grasslands are gently undulating and host a variety of insects, and non-flooded portions of the grassland with their termite nests constitute the

TABLE 4.2
Definitions of *niche* and examples of conceptual diversity

Definitions and examples	Reference	Additional comments
A niche is an evolved, multidimensional attribute of a particular species population.	Whittaker et al. (1973)	This definition is compatible with the use of ecological characteristics of a species. It also precludes the amount of resource from being a part of the hyperspace.
A niche can be defined by the relations of a species with other species of the community.	Herbold and Moyle (1986)	Cited view.
A niche is an N -dimensional hypervolume enclosing the complete range of conditions under which an organism can successfully replace itself; every point of hypervolume corresponds to a set of values of the variables permitting the organism to exist.	Hutchinson (1957)	Vague on the resource amounts; it is easy to imagine that it sets a minimum resource level for a viable population, but because there is no upper limit to the amount of resource available, one should not interpret this definition as fully permitting resource amounts. Indeed, adding the resource amount as one of the axes would render the niche volume infinite from a mathematical perspective.
Niches are preexisting properties of the communities and their environment.	Giller (1984)	Cited view. It corresponds more to the HBM concept of habitat than to species attributes.
The range of values of environmental factors necessary and sufficient to allow a species to carry out its life history.	James et al. (1984), citing Grinnell's ideas	Niche defined by species requirements.
The representation of the population niche would consist of a cloud of points in phase, the more favored parts of the niche being represented by an increased density of points.	Wangersky (1972)	Niche defined by species performance on an environmental template. If points (individual organisms) are described by values of habitat axes, then this concept corresponds closely to the realized niche.

TABLE 4.2
Continued

Definitions and examples	Reference	Additional comments
The set of all observations of an organism in a m ultidimensional hyperspace can be thought of as the observed niche (with a probability function suggested as the mathematical approach to niche description).	Silvert (1994)	'This view is close to the concept of realized niche. The fundamental niche, although addressable via evolutionary perspective, is not always definable through observation because a species may never be tested over the potential range of environmental values.
No explicit definition given. In the simplest terms, Leibold conceptualizes niche as two interacting sets of dimensions: those pertaining to species requirements and those describing species impact on the environment.	Leibold (1995)	This approach attempts to deal with the quantity of resources (and related factors), which was missing from other conceptualizations of the niche. It is not clear if the niche is a characteristic of species or a new conceptual entity incorporating "impacts."

anteater habitat. Landscapes of flood-free grasslands, and the density, distribution, and quality of termite nests constitute habitat structure.

The community habitat space is likely to coincide to a substantial extent with portions of the environmental template that are homogeneous (homogeneously diverse *sensu* Hutchinson 1957) relative to the surrounding matrix. This is not because the two are conceptually the same but because of the evolutionary history and adaptive responses of species. A lake is a relatively homogeneous patch of environmental template by most criteria. All fish species are likely to find their habitat spaces (or, simply, habitats) within that patch. Consequently, the habitat as identified by species is different from the full complement of variables the environmental template would require for description; a species "carves out" a habitat from the overall volume. Despite this difference, the habitats selected by species should generally coincide with the basic subdivisions of the environmental template, subject to empirical verification. This permits us to present views on the structure of habitat without constant distinctions between the species perspective and that of the external observer (the ecologist).

Model Structure and Requirements

The model requires that a habitat unit—a community habitat space—be identified. By defining a unit using all the species in a community, we create a reference level for habitat subdivision. Thus, the habitat unit is the highest level. There are practical reasons underlying the decision to have a large unit. The most important characteristic of this space is that it spans the full range of ecological conditions experienced by the species in question. The model permits the use of arbitrary habitat units, that is, units defined without a prior evaluation of the relative homogeneity of habitat. Such units may, however, introduce biases resulting from improper scaling (Addicott et al. 1987). The biases would emerge because the model relies on determination of ecological ranges of species, which would likely be incorrectly represented when using arbitrary habitat units.

Any habitat unit, whether a pile of dung, a lake, or a mountain range, is composed of subunits, which can be split into even smaller subunits. The criteria for distinguishing subunits are provided by species perception of boundaries in their environmental template which, as suggested earlier, are likely to correspond to the natural subdivisions of that template. The resulting subdivisions are a function of the perceptual resolution (whether by species or investigator). Low resolution yields coarse, high-level subdivisions, while high resolution identifies fine, low-level habitat subdivisions (figure 4.4). Criteria for subunit demarcation need not be invariant, and they can change from level to level. For example, at the highest level, the distinction may be made between water and land. When we analyze aquatic habitat (Pahl-Wostl, chapter 7), the criterion may be temperature, which separates the epilimnion from the hypolimnion zone of a lake. Such criteria are clearly scale dependent but fairly easy to identify and use. Scale-independent criteria exist and involve the magnitude of unit integration (Kolasa and Pickett 1989). However, these criteria are difficult to apply because methods for making them operational have not been sufficiently developed.

One striking feature of the model of habitat structure is nestedness. Smaller, low-level units are nested within larger, high-level units. This nestedness has potentially important consequences for constraining species activities and interactions and for creating differential species links to the environment. Consequences of nestedness on species performance will be discussed later.

Assumptions: Relationship Between Species and Habitat

The general assumption is that species interact with habitat and that this interaction has a number of detectable consequences for species abundance, selection of life strategies, probabilities of extinction, distribution patterns, and other ecological phenomena. The interaction of species with habitat is primarily via species tolerance limits, habitat variation, and habitat structure. Tolerance limits determine whether a species can live in a particular habitat. Habitat variation may influence species persistence through generation of temporarily adverse conditions, and the habitat structure interacts most visibly with population cohesion and individual mobility. Habitat structure and variation may have equilibrium and nonequilibrium components. For example, monkeys in seasonally flooded forest of the Amazon River drainage utilize different food resources during the flood and dry seasons. This seasonality determines the range of some species. Within the range, food availability is subject to asynchronous fruit-bearing by trees and to a patch disturbance regime. This nonequilibrium component of habitat

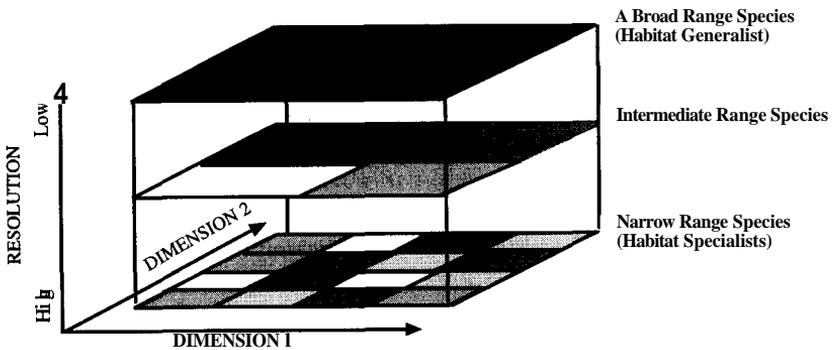


FIGURE 4.4

A conceptual model of habitat structure in which homogeneity and heterogeneity depend on the resolution with which species perceive their environment [modified from Kolasa (1989)]. The top level appears homogeneous and can be occupied by only one species. Levels below, which represent successively higher resolutions and smaller habitat grain, reveal mosaics of different microhabitat types and can, correspondingly, be inhabited by more species. Habitat of species using lower levels is more fragmented. In the HBM, specialization is correlated with the degree of habitat fragmentation, with the correlation strength dependent on variation in the actual arrangement of patches.

structure may be as important as the seasonality itself to the success of some species and the failure of other species.

Species perceive their habitat at different scales of resolution and respond to spatial scales at different levels (Kotliar and Wiens 1990; Milne 1991a; Sagova and Adams 1993). These differences make species that occur in the same locality live in different universes and interact with each other under different rules (Waltho and Kolasa 1996; Allen, chapter 3; Martinez and Dunne, chapter 10). The relations among species and their habitat include both static and dynamic links.

Differences in ecological requirements define the kind and hierarchical level of habitat unit a species can use. The view of specialization outlined earlier may now be combined with the hierarchical structure of habitat. Specialists use small subdivisions of the habitat and can be pictured as using lower levels of the hierarchy (see figure 4.4). Generalists use composite and thus larger fragments of the same structure and appear at higher levels. Size of the habitat portion is relative to the ecologically broadest species and should not be confused with the absolute size of two-dimensional patches (Forman 1995). This separation corresponds with the opposite levels of perceptual resolution. Specialists are high-resolution species, whereas generalists are low-resolution. Consequently, generalists often appear as coarse-grain species and specialists as fine-grain (Kotliar and Wiens 1990). However, the terminological distinction between coarse-grain species and habitat generalists is still required, because the first term refers to spatial fragmentation and patch size, whereas the second term refers to the number of habitat categories used, irrespective of their spatial arrangement; the two aspects are correlated but not the same. The difference between habitat generalists and coarse-grain species is related to the scale of perception and the scale of habitat heterogeneity. In simplest terms, one may consider a community where only one species is permitted to occupy a particular habitat subunit distinguished at a given hierarchical level. By definition, a subunit is homogeneous at that level, and thus, any two species using it would have to use identical resources and face severe competition. The competitive exclusion principle does not allow more than one species to persist in such an environment (Murray 1986a), although this is an idealization.

In natural systems, one would not expect perfect correspondence between habitat units and their respective species. First, species are not “perfect,” because species associations with some habitat dimensions are probabilistic rather than deterministic, and even unsuitable areas of habitat space may be subject to exploratory colonization or

establishment (Wu and Vankat 1995). Second, the habitat unit is assumed to be homogeneous at a particular scale of resolution, although scales of resolution may be incompletely isolated from each other from the species perspective. Some individuals may perceive more local (unit) heterogeneity than others, which may affect habitat use and result in variable competitive ability. Third, the species–habitat relationship may itself be far from equilibrium, especially at some scales or in some habitat units. In these situations, the model may perform inconsistently unless factors interfering with the dynamic equilibrium are taken into account (Wu and Loucks 1995).

Species' associations with their respective habitat units form through a variety of mechanisms and their combinations. In the terminology of the HBM, the habitat resolution of a species is a function of the species' association with a particular habitat subunit. Prohibited habitat is invisible habitat. As some limiting conditions are removed, species may move to habitat units previously unavailable, which produces a change in the level of habitat resolution. Finally, we must address additional complexity stemming from ontogenic habitat shifts. Many species change their requirements and habitat resolution as they develop from seedlings, eggs, and propagules into adults. While a full characterization of a species implies taking into consideration all these stages and their relationships to habitat, a number of ecological questions that can be addressed by the HBM need not involve all life stages for all analyses. The HBM is most effective when applied to a life stage that is most limiting to the population size. If the limiting life stage is survival of the young, then one should concentrate on the habitat structure as perceived by that life stage. If the limiting life stage is the habitat needs of the mature stages, then the autecology of juveniles can be ignored. Empirical work is needed to determine which is relevant before a general model is applied. The model itself could be used to determine the relative importance of the life stages in determining population size and distribution; its predictive power can be calculated independently for different life stages.

Predictions and Explanations

The strength of the HBM is its large range of mutually supporting and reinforcing applications. The HBM (1) explains patterns other models do not address, (2) allows a number of unique predictions, (3) agrees with successful explanations provided by other models, and (4) ex-

plains why various models apply at various scales (Tokeshi 1993). Other models cover but a fraction of the issues the HBM solves and identifies. Some examples will be discussed.

Patterns Not Addressed by Other Models

Rank-abundance curves range from a straight line to an S-shaped curve. These empirical distributions have stimulated the development of models based on fitting various mathematical functions. The two extreme forms involve the geometrical distribution and lognormal distribution. Biological motivation for these distributions is weak or non-existent, depending on the model (Motomura 1932; Sugihara 1980; Ugland and Gray 1982; Magurran 1988). The HBM predicts the geometric distribution in simple (low dimensional) habitat units, such as in a conifer plantation (Magurran 1988) or those created by major disturbance; a lognormal-like distribution can be appropriate in more complex habitats or at large spatial scales. In complex habitats (see figure 4.4), species abundances are determined solely by scaling of one criterion. If space is the criterion, then the simplest subdivision of a habitat unit will result in two, then four, then eight subunits, and so on, with species abundances following a similar pattern.

In high-dimensional habitats, with many criteria involved and varying across levels, lognormal distribution of abundances is expected because random variation in many factors will tend to result in a normal distribution of abundances (May 1975; Magurran 1988). For example, a model that assumes seven species, with one species at the highest level, two at the intermediate level, and four at the lowest level, and that assumes (1) equal access to resources and (2) a three-to-one ratio of species occupying the same habitat unit (Sugihara 1980), produces a nearly straight linear fit ($r^2 = 0.9428$, $P = 0.0003$, $N = 7$) (table 4.3). This interpretation agrees with concepts proposed by Tokeshi (1993), who linked the pattern gradient from geometric series to lognormal series to the scale of sampling. Similarly, the HBM predicts the lognormal-like distribution of abundances at larger organizational scales in contrast to scales allowing analysis of single, small habitat units, because large-scale patterns are likely to involve a greater range of causal factors. Finally, in homogeneous habitats, one would expect species abundances to be determined by priority effects (niche-preemption model; Whittaker 1965), or by random processes if no priority effects apply (broken stick model; MacArthur 1957). Thus, the abundance distribution is not just a statistical product of multiple in-

teracting variables (May 1975) but an explicit product of hierarchical habitat structure and unit size (see figure 4.4). The model predicts that simple structures produce straight rank-abundance lines, whereas rich structures produce S-shaped curves. In this sense, the model agrees with extensive ecological evidence that patterns of abundance differ among habitats, sampling scales, and patterns of disturbance.

Unique Predictions

We identify two unique predictions of the model: one about the discontinuities of community structure and the other about the effects of wrong scale on model accuracy. These predictions are a powerful testing ground for the conceptual foundations of the model. To the extent they have been verified, they provide substantial supporting evidence for those foundations. Consider two adjacent hierarchical levels of habitat. A species has a choice of using either the higher-level unit or

TABLE 4.3
Example of calculations for a simple, seven-species model*

Species 1 (1)			
Species 2 (.75)		Species 3 (.25)	
Species 4 (.56)	Species 5 (.19)	Species 6 (.19)	Sp. 7 (.06)

1	1.00	1.00	1.00	49.58
2	0.75	0.75	0.563	27.91
3	0.25	0.25	0.063	3.12
4	0.563	0.563	0.317	15.72
5	0.188	0.188	0.035	1.74
6	0.188	0.188	0.035	1.74
7	0.063	0.063	0.004	0.20

*Consider a case of seven species constituting the community shown. Size and position of the boxes represent relative ecological ranges and position in the habitat mosaic for each species. Proportions of the ecological range are shown for each species (e.g., the proportion for species 7 is **0.06**). The size of the boxes is the mean random value attained by a species if it consistently acquires either more or fewer resources (Sugihara 1980). In this simple case, specialization assumes values identical to those of the range, but this is not necessarily true for data from natural communities unless the broadest species occurs throughout the whole measured range of values.

** Specific calculations for this part of the table assume equal division of resources among hierarchical levels. For communities in which data suggest a different division, the proportion of habitat values should be multiplied by a coefficient associated with a particular level.

one of its subdivisions at the lower level. Depending on which level the species is able to choose, the amount of available habitat differs dramatically. Because several species face similar choices at approximately the same levels of resolution, a natural division is likely to occur. Some species will occupy higher-level units and others the lower-level units. This should result in an emergence of species groups characterized by similar position in the structural hierarchy of habitat. Because the level at which a species operates predictably affects its abundance, species sharing a level should also fall into the same abundance classes. Thus, in addition to a positive relationship between ecological range and abundance, one could also postulate distinct discontinuities in parameter values (figure 4.5).

The second prediction is that if the scale of sampling is too small relative to the extent of ecological range required by the model for the analysis of a particular community, then the relative abundance of generalist species will be underestimated and the abundance of special-

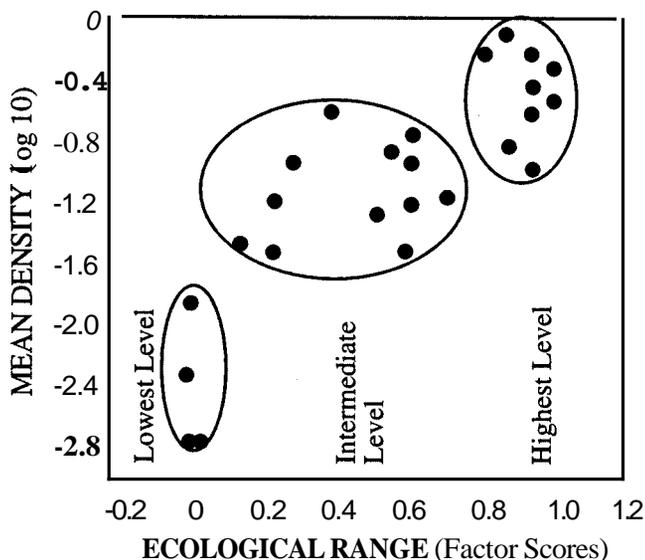


FIGURE 4.5

An example of discontinuities in species ecological range: each circle is an invertebrate species inhabiting a system of small rock pools on the northern coast of Jamaica. Ecological range is based on the maximum ranges of oxygen, salinity, pH, and light experienced by a species over 49 pools.

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ist species will be overestimated. This poses a problem for study design, because it is not immediately obvious which scale is appropriate, at least not before the data are available (see also chapters 12 and 18 of this volume). The test of this prediction can be conducted in communities in which the ecological range of the top habitat generalist is known or possible to assess prior to the test. Alternatively, one might keep expanding the observation set until the range of conditions sampled is equal to or broader than the range observed for the broadest of species (Waltho and Kolasa 1994). In such a situation, one should initially observe an increasing trend in the estimated relative generalist density. This trend should stop after the expanding data set includes or exceeds the ecological range of the broadest species. The breakpoint in a regression could be used to identify the proper scale for a community in question, and this scale should coincide with the range of the broadest species. To the best of our knowledge, no other model predicts the above patterns.

Study Design and Methodological Concerns

Operational Approaches to Habitat Units

The preceding paragraphs imply that knowledge of habitat structure is important for the analysis of interactions among species and their habitat (unit). We envision an extensive set of rules on how habitat structure can be determined and evaluated. Common ecological sense may be the best guide. Given the definition of the habitat, however, one logical approach would include the following steps:

1. Identify dimensions of relevance to the species present (e.g., predators, resources, physical conditions).
2. Create a multilayer map representing distribution of the values for each dimension on the landscape of interest.
3. Superimpose individual species requirements (“niches”) on the map to assess the configuration (fragmentation, amount, distribution) of its habitat space and nestedness relative to other species.

A simpler, acceptable approach is to measure the distribution of species over the habitat space and deduce habitat structure from it. Distribution of species over the habitat space can be measured along one or few dominant variables, or, even more simply, in physical space as long as the physical space reflects some gradient of habitat qualities. For aquatic invertebrates occupying rock pools, distribution in space

correlates strongly ($r^2= 0.88$) with composite measures of habitat variables (Kolasa and Drake 1997). For example, one can assess species distribution in a two-dimensional space of phosphorus and nitrogen concentrations, which might be appropriate for aquatic algae or along mountain slope sites that encompass a multivariable gradient. A species present at many sites defines a larger habitat unit than a species living only in the subalpine zone, a smaller habitat subunit.

Although the definitions of both habitat and species hypervolume refer to and rely strongly on multiple dimensions, the task of quantifying these concepts in the field is less complicated than the concepts might imply. This is because of two premises. First, any dimension relevant to species performance will map in space. Even such esoteric variables as predation risk will have spatial representation. Second, most variables are spatially integrated. For example, a clump of shrubs in a savanna has different food resources, risk of insect bites and infections, thermal and humidity regime, mate encounter, detection probability, and sun exposure than an adjacent patch of grass. It is possible to use only a limited number of measurements for assessing habitat structure, because many of these variables are correlated.

Scaling of Sampling Protocol

Because the primary application of the HBM is to examine differential performance of species over their habitat, it is important that the analysis does not underestimate or overestimate the habitat space of any of the species being compared. This requires that sampling should cover the range of values (for the variables one decides to analyze) that equal or exceed the range of the ecologically broadest species. It also requires that the sampling resolution is equal to or higher than the habitat grain to which the ecologically narrowest species responds.

In addition to the need for adequate scale for testing the model, other considerations may become important under some circumstances. As mentioned earlier, different scaling will result in different rank-abundance patterns (Tokeshi 1993). Thus, application of the model to areas differing in size or heterogeneity will result in data of different usefulness for testing specific predictions.

Summary

The HBM overlaps with other models to a varying degree. For example, the habitat specialization aspect is shared with Brown's (1984)

model. Aspects of habitat fragmentation and patchiness are similar to the core–satellite model (Hanski 1982). In fact, each resolution level could be considered a landscape of patches in which species play out their patch occupancy game. The hierarchical subdivision of resources is conceptually similar to the sequential breakage model (Sugihara 1980) and is consistent with other resource-partitioning algorithms. Putnam (1994) supports Ugland and Gray's contention (1982) that the canonical lognormal curve arguments of Sugihara are wrong and that data actually refute them. If this is so, then this particular model of niche partitioning should not be legitimately compared to HBM. Nevertheless, other niche-partitioning models might be viewed as special cases of habitat structure perspective (Tokeshi 1993) in which resource availability declines with the size of the habitat unit used by a species. However, there is more than niche space to determining of species abundances. Indeed, a fully quantitative version of HBM would require formulae that combine scaling effects of increasing habitat resolution (specialization), such as reduction in available habitat, penalties of fragmentation, and allometric trends (Nee et al. 1991) associated with habitat size and differential patch dynamics (Collins and Glenn 1991). Page1 et al. (1991) analyzed 72 natural communities and found that relative abundances of species do not necessarily reflect division of resources. They further found that smaller species use substantially fewer resources than anticipated from allometric considerations alone. Coincidentally, Brown and Maurer (1986) estimated that habitat generalists, despite being generally larger and fewer in numbers, command more resources on a habitat-unit basis (thus reinforcing the notion of greater success of generalists). These two studies jointly suggest another factor—habitat structure—that determines the performance of species on an environmental template. Tests of the model should thus involve either a complete account of all these aspects or create conditions that permit controlling for some of them.

Although the HBM shares different assumptions and mechanisms with several other models, it is not a specialization hypothesis, a version of the core–satellite model, a heterogeneity-based explanation, or a niche-partitioning model alone. None of these assumptions and hypotheses alone sufficiently represents the consequences generated by the HBM. The specialization hypothesis does not consider scaling of habitat fragmentation, the heterogeneity perspective is incomplete without multiple levels of resolution and patch dynamics, and the niche-partitioning models have little to say about consequences of habitat structure.

Gaston and Lawton (1990) note that the distribution–abundance relationship may be negative when the habitat considered is rare in the region but positive when the habitat is common. In the HBM, the species ecological range is measured as a function of its use of the multi-dimensional habitat space. If a species has a broad ecological range, it will occur in most habitats of the region and thus cannot be affected by the habitat rarity unless an extremely common habitat type also has extreme attributes. In the HBM, the broad range correlates positively with abundance. If one defines ecological range at a scale different than the data used to evaluate it, or in some other arbitrary way, then spatial fragmentation must be considered separately and is likely to lead to the observation made by Gaston and Lawton (1990). In the HBM, a species should not be considered a generalist (broadly distributed) when it lives in a small fraction of available habitat types. Consequently, the observation is precisely anticipated by and consistent with the HBM: the geographical or spatial aspect of habitat fragmentation is subsumed in the definition of specialization and thus needs no explicit attention.

The HBM brings together important features of various models and hypotheses and places them within a single framework of the species–habitat relationship. By doing so, it frees those models from their scale blindness, permits addition of new mechanisms, and provides a context for evaluating the relative importance of various processes (Kolasa and Drake 1997). The species–habitat relationship is a more general type of relationship than the species-to-species relationship, which can be realized only in the context of the species–habitat relationship.