Patterns of the abundance of species: a comparison of two hierarchical models

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We compare two hierarchical, predictive models that explain the log-series pattern of distribution of species abundances. The Sequential Breakage Model (SBM) is based on the appropriation of fragments from the community niche volume, while the Habitat-Based Model (HBM) assumes a contemporary use of environmental volume by species acting in different scales. A detailed analysis of assumptions of the SBM indicates that its predictions rely on the establishment of a link between the niche overlap and abundance of species. We show that this link is inadequate and may be incorrect. The agreement between the abundances predicted by the SBM and the abundances observed in assemblages composed of three species cannot be thus considered as validation of this model. We conclude, however, that such an agreement supports the Habitat-Based Model. The predictions of the HBM are generated from a realistic combination of commonly observed ecological phenomena (habitat heterogeneity and patchiness), species properties (differentiated degrees of specialization), and the assumed relation between them. The latter model is sensitive to habitat heterogeneity. This difference may be used in testing both models under different ecological conditions and at various scales.

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Introduction

A leading question in ecology for the past 30 years has been: "what are the reasons for ubiquity of the log-series and log-normal distribution patterns of species abundances?" Earlier explanations (Patrick et al. 1954, Preston 1962, Whittaker 1965, May 1975) have been challenged recently and succeeded by several new propositions (e.g., Brown 1984, Ugland and Gray 1982), two of which include a hierarchical view of the world as necessary to understand the pattern, but which differ in other important aspects. One is a sequential breakage model (SBM) suggested first by Sugihara (1980) and later expanded (Sugihara 1983), and the other is the habitat based model (HBM) proposed by Kolasa and Biesiadka (1984).

These two models differ in the method by which they partition hypothetical abundances, and especially in their assumptions as to underlying biological mecha-

nisms. Here we critically evaluate the two models and propose conditions for a test between them.

Sequential niche breakage model

The sequential breakage model explains the log-normal distribution of species abundances as a result of a gradient in species specialization which is termed "a hierarchy of niche similarities". According to the model, such a gradient might arise as a result of either evolutionary or ecological mechanisms through subsequent additions of species, leading to sequential breakage of the community niche volume.

In this model the volume of the communal niche space is sequentially split up by the component species as they are added to the community, so that each fragment denotes relative abundance of species (compare MacArthur's broken stick model, MacArthur 1957). The magnitude and frequency of breaks are assumed
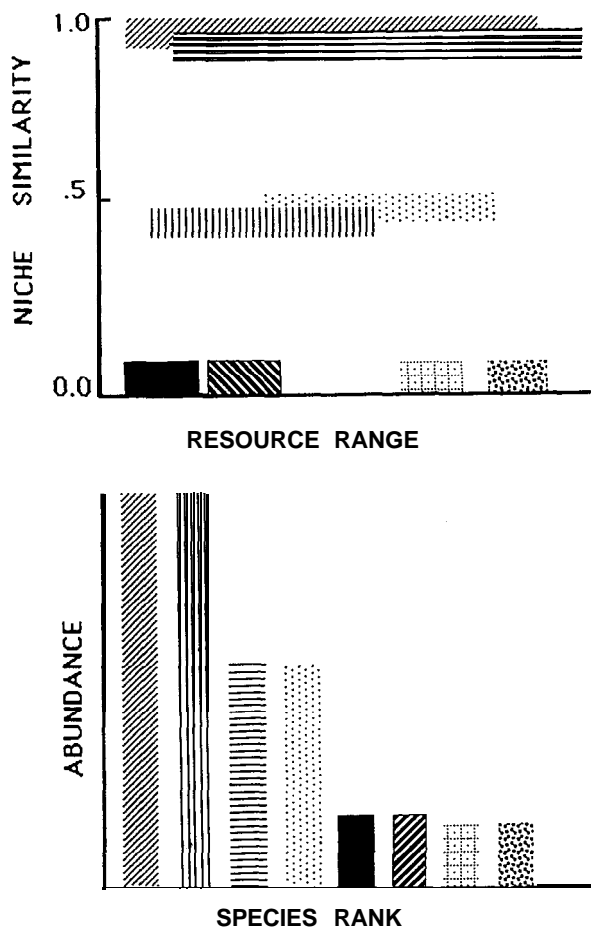
Fig. 1. Examples of possible relationships between pairs of species in a two-dimensional space (resource use, overlap) and corresponding abundances (if abundances are presumed to be proportional to the amount of resource used).

independent of the sizes of individual species niches, i.e. large niches are as likely to undergo a split by the next species added to the community as small niches. If any of the presently occupied niches is split up by a new species, the two resulting niches are smaller, the two species that occupy these niches are considered a tightly related functional group of species, and the niches themselves are viewed as the most similar. The SBM is based on the following explicit (l-5) (Sugihara 1980, 1983) or hidden assumptions or statements (6-7):

1) The pattern of the relative abundance of species is based directly on the underlying structure of niches.
2) The niche structure for communities is hierarchical. By the niche structure Sugihara means the pattern of niche similarities (see 3 and 5 for more information).
3) It is possible to cluster species niches by increasing niche similarity (defined in 7) into natural groups.
4) With the increase in niche similarity the niches become smaller and the abundance of the corresponding species will be smaller as well (see 1).

5) Subdivision of the niches is dichotomous: at each subsequent point of classification a part of the communal niche volume (the total niche requirements of a community in Whittaker's [1977] sense) is subdivided into two portions. In practice this means that an earlier established species has to share parts of its former niche with the new species. Such niches as well as species are considered by Sugihara as similar.
6) Relative niche volume of one species (and therefore its relative abundance – assumption 1) is directly dependent on the niche volume (= abundance) of all other species involved in the breakage sequence since any break in the niche volume of a species subtracts some volume from its current value. At the same time the niche volumes of other species remain unaffected. Thus, the sequential partitioning must necessarily reflect competition. Sugihara's model does allow an expansion of the total communal niche volume, however (Sugihara 1980: Fig. 3).
7) Niche similarity is proportional to niche overlap.

Results from Sugihara's model are extraordinarily similar to real data gathered on the relative abundances of species from natural communities. Yet, despite the close fit of model output to real data, there are some theoretical problems with this model.

The central problem with Sugihara's model is the linkage between niche volume and abundances of species. There seems to be a contradiction between assumption 5 and assumption 7. Under assumption 5 the similarity of niches is determined by the proximity of the niche formation in the sequence of breaks, i.e. when the original niche has been split into two descendant niches; recent splits identify similar niches. Under assumption 7, however, the similarity of niches is determined by the degree of overlap. Below we present arguments that under certain, and not necessarily rare, circumstances these two assumptions are incompatible. Sugihara (1980) argued that similar niches, which were formed by frequent breaks within one niche cluster, must have small volumes and consequently lead to low abundances. He defined niche as "an n-dimensional resource set," where "the only non-trivial connected regions consist of those species niches that overlap on, and are *completely* represented by, a common set of resources axes" (Sugihara 1983). This definition does not take into account the quantity of resources, only the quality. Resource quantity is a variable that cannot be represented as a property of the species per se. However, resource quantity can determine, in the absence of other limiting factors, the absolute upper limit of the species' abundance. Consider for example a granivorous generalist feeding on all available seeds in a forest habitat. If a very similar species colonized the same area, the two species would have almost identical niches but the amount of resource per species, and thus their abundance would be reduced. The overlap in their resource use would be full. However, if in the course of

evolution these two species would specialize to two different spectra of seeds, the overlap and similarity over the axis of the resource use would disappear but abundance would not change if compared with the situation when there was a full overlap. Even if we treat resource amount as a niche component, two species cannot overlap along this axis; they can only complement each other in the use of the available resource. The respective niche volumes of the two species may shrink along all other axes as the species become more specialized ecologically, without a corresponding change in their abundances, which will depend on the amount of resource used. The relationship between the niche volume and abundance of a species is thus obtained in two steps. The first of these steps equates the niche volume with the resource range, and the second step links the resource range with the resource availability. Such a link, however, although plausible in some situations, cannot be considered as a general and necessary consequence of Sugihara's assumptions. These same assumptions permit opposite results where a greater overlap is associated with greater niche volume and greater abundance. Fig. 1 illustrates the point. Species A and B overlap over the whole range of the resource and therefore have maximum similarity (assumption 7), should represent a small, "tightly related functional" group (assumption 4), consequently should have small niche volumes and lowest abundance (assumption 1 and 6). We see, however, that even if we satisfy the assumptions of the model, it is easy to conceive of situations where the assumption 7 contradicts diametrically results predicted from assumptions 1 and 6 (e.g. niche similarity may increase, and likewise the abundances, with the widening and overlap of individual niches, while the SBM demands that the abundances decrease with the increase in niche similarity).

We thus conclude that the relationships invoked by this model (and necessary for the model to work) between the niche volume and abundance and between the niche volume and niche overlap, have been shown to lack evidence and can lead to potentially contradictory conclusions. This is understandable in view of the basic niche concept (Hutchinson 1957, Sugihara 1983), which is a projection of properties of a species into ecological space; i.e. the "ecological morphology" of a species. Environmental features such as the *supply* of a resource are not parts of the "ecological morphology" of a species and are not explicitly included in the basic concept of the niche. This conceptual disjunction within Sugihara's niche model prevents its formal use for predicting species abundances.

The SBM shares another weakness with several other formally motivated models: it is not sensitive to differences between homogeneous and heterogeneous habitats. It has been stated frequently that more homogeneous habitats tend to have dominant species relatively more abundant than they are in heterogeneous habitats (e.g., MacArthur 1958, O'Neill 1967, Abele 1974). Yet,

the SBM does not have a mechanism to respond to such differences. Instead, the predictions of the relative abundance of all species, including the dominant, are a function of a single factor, species number, in a fashion that seems unrealistic.

Sugihara (1980) thought there is a link between the canonical log-normal distribution of abundances and the species-area curves, which indirectly supports the premises of his model (see also Preston 1981). This link is explainable, in his opinion, if the model is correct. However, the suite of statistical arguments supporting the sequential breakage model has been rejected, or questioned, by Connor et al. (1983), Harmsen (1983), and Ugland and Gray (1982), who argued that the log-log species-area curves do not require an ecological explanation since their specific property (slope values) is expected independently of the biological grounds. Furthermore, Harmsen (1983) provides new data that are inconsistent with the canonical hypothesis. Brown and Maurer (1986) show that energy partitioning among species leads to a log-normal distribution which will not be canonical (Harvey and Lawton 1986).

Habitat-based model

A detailed description of this model, together with new insights, is presented elsewhere (Kolasa 1988) and therefore we limit its presentation to an outline only. In the habitat-based model (HBM), the chief role in generating log-series and log-normal distribution is attributed to the hierarchical nature of the habitat. Each distinct fragment of habitat may be subdivided into smaller fragments according to a biologically significant criterion. If each hierarchical subdivision is occupied or used by a species, the entire collection from that community will necessarily display the log-series pattern of abundances. Such log-series distributions, if added up, will approach a log-normal distribution of species abundances (cf. May 1975, Ugland and Gray 1982).

We use the habitat-based model to interpret abundances of species as the direct result of interactions between populations of different species and environmental structure. Here, some species (generalists) are thought to occupy the comparatively large portion of the habitat, while others occupy only parts of the habitat (specialists). The habitat is not restricted to spatially defined entities but it also includes other ecological dimensions. There may be several levels of subdivision of the habitat allowing several levels of species specialization. The generalists will be thus much more abundant than the specialists because of the small amount of habitat available to specialist whose habitat size will shrink rapidly with each hierarchical subdivision. This model is based on the following specific assumptions (Kolasa and Biesiadka 1984):
1) Species differ in their degree of preference and tolerance for environmental variables, whether these variables are resources or physical gradients.

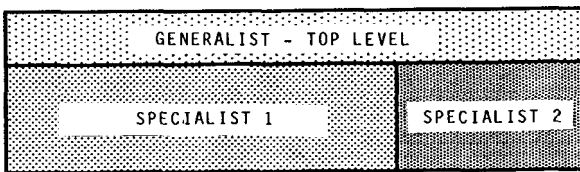**80:20**

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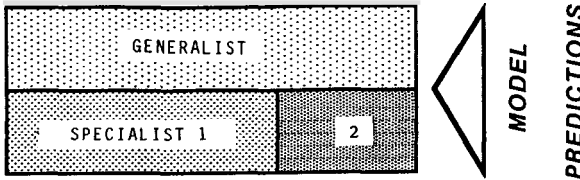
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Fig. 2. Possible resource allocations between two levels in a three species community resulting from different species efficiencies. Each compartment represents the share of resources used by **a** species at the specified efficiency levels. For example, in the top case the generalist has the efficiency of 80% and the two specialists have an average efficiency of 20%. Only the case with even allocation is used in further calculations. The generalist uses the whole range of resource (operates at the higher level of organization). Two specialists share the same resource with the generalist, but not with each other (operate at a lower level of organization).

2) Generalists can use a wider spectrum of resources, space or time range, than specialists.

3) A species should be (on average) more abundant if it is able to use a broader spectrum of resources (Pielou 1975, May 1976, Whittaker 1977) or if it is able to survive a broader range of physical conditions.

4) The environment can be viewed as hierarchical, that is, any unit of the environment (including both biotic and abiotic variables) can be regarded as being composed of subunits, and these subunits may be composed of smaller units. For example, a stream bottom is composed of mineral and organic substrates; mineral substrates are composed of several size classes of rock usually deposited as distinct bars; similarly organic substrates such as leaves, twigs, algae, pellets, and silt accumulate as patches of different size composition, origin, and texture, each being composed of even smaller patches. Relevant unit boundaries are shaped by species resolution and responses to habitat heterogeneity and thus can be determined by investigation of the habitat/community relationship.

The assumption of the hierarchical nature of the environment leads directly to two important consequences. One is that with each level of subdivision the environmental units become smaller than a higher unit. This observation is not limited to the physical dimensions only. Indeed, ecological dimensions such as predation. competition, quality and diversity of resources would behave in a similar way and result in analogous consequences. In case of variables describing environmental ranges, subdivisions will lead to narrower ranges. The second consequence is that the more specialized the species, the smaller the physical and biotic environment it can use. This, coupled with assumptions 3 (and 4). results in higher abundance of generalists over specialists (on average again) and, if coupled with assumption 4, predicts a distribution of abundances resembling the log-series. A log-series results because the nested hierarchy of environment leads to exponential decrease of the size of subunits in the hypothetical multidimensional ecological space. In other words. each subsequent sub division of habitat may generate a corresponding group of species. As one moves to lower subdivisions. the groups will contain more species with much lower relative abundances (Kolasa and Biesiadka 1 9 8 4) Ugland and Gray (1982) used similar, although arbitrarily defined, groups in their explanation of the log-normal distribution of abundances.

Thus, the HBM provides an ecological mechanism for generating the various patterns of species ahundances. Because the model is based on the hierarchy of environment, it follows that different environments will result in different distributions of species ahundances. Such distributions may display various mathematical properties (cf. Whittaker 1965). not only the unique log-normal distribution suggested by Preston (1962) or Sugihara (1980). To the extent that specific environmental structures underlie the pattern of species abundance, a search for a single simple mechanism to explain the log-normal pattern will be unproductive. May (1975) indicates that the log-normal type of distribution is to be expected, in accordance with the Central Limit Theorem, in all additive statistics, including the l o g series. However, Routledge (1980) questions this view on the mathematical basis. One might speculate that although the elementary distribution of abundances resembles log-series in the HBM, abundances of species in large collections from natural communities would often be distributed log-normally because of either the numerical size of the sample or internal heterogeneity in the sample (cf. May 1975, Rejmanek, pers. comm.. but not Sugihara 1980) (i.e. in cases when the sample includes more than one hierarchical unit of environment).

Testing the models

Despite the apparent complexity of the two models. it is relatively easy to identify conditions under which model predictions differ. It will be convenient to demonstrate

Tab. 1. Specific numerical assumptions of the HBM used in prediction of relative abundances for three-species assemblages. Notice that, as assumed in the text, the average relative efficiency for the two specialists is the same as for the generalist.

Species	Habitat use (range, R)	"Dilution factor" (D)	Relative efficiency E	(E)
G	𝟙 (entire)	1	0–1.0	(=0.5)
Sl	1/2 (half)	1/2	0.5–1	(=0.75)
S2	1/2 (half)	1/2	0–0.5	(=0.25)

Tab. 2. Data used to calculate relative abundances in the three species assemblages (taxonomical collections from one site).

Data source	Taxon	Pl	P2	P3	N
Dayton 1971	Limpets	0.546	0.321	0.133	13
Dayton 1971	Barnacles	0.703	0.211	0.086	13
Dayton 1971	Gastropods	0.646	0.228	0.093	10
Wappinger*	Flatworms	0.671	0.251	0.081	10
Wappinger*	Insects	0.656	0.257	0.087	19
Poland/PNG**	Flatworms	0.695	0.226	0.078	25
	Model	0.667	0.250	0.083	

* from the East Branch of Wappinger Creek, Millbrook, New York (Kolasa et al., unpubl.); data available from the first author upon request.
** from all sites together in Poland and Papua New Guinea (unpublished or partly published in scattered references by the first author); data available upon request.

this by an example. Our first example is generated for three species to make direct comparisons with the SBM for which calculations have been made by Sugihara (1980).

For an assemblage of three species, a minimum underlying hierarchy of environment requires two levels and three units, one unit of environment at the higher level (U) subdivided into two equal subunits (SU1) (SU2) at the lower level. Each of these units is occupied by a species. A species using the higher level unit will be called a generalist (G), and two species using the subunits of the environment will be called specialists (Sl and S2). We assume that each of the three environmental units provides the amount of usable resources proportional to the size of unit. We further assume that the specialists are not different in their efficiencies of resource use from the generalist. Like fitness (see Rosenberg 1985: 155), efficiency is meant here as a relational property, reflecting the interaction of an average organism and its environment. We also assume that the SU1 and SU2 have similar sizes and frequencies of occurrence. and that they are evenly interspaced. Yet, we assume. that the specialists differ between them in the way they use their respective resources and, consequently. in their abundances. It follows from the last assumption that the less abundant species will have the relative abundance value in the interval 0-0.5 (0.25 on average) and the more abundant species will have the abundance value in the interval 0.5-l (or 0.75 on average) (cf. Sugihara 1980). The concrete example below could illustrate various ecological situations; for instance pollinators using flowers in a garden, lower invertebrates colonizing microhabitat islands, plant dispersal over hostile stretches of land, or rodent populations moving among a mosaic of landscape types.

Example. Three species of insects (G, Sl, S2) use two species of flowers (Fl, F2) which correspond to our earlier subunits SU1 and SU2. All flowers together represent the higher level unit of environment (U = Fl – F2). One of the insects (G, a generalist) can use both flowers (Fl + F2). while the two others (Sl and S2) are specialized to one flower each. Because the density of flowers available to the generalist is twice as high as those available to each of the specialists, the energetic

and population costs of specialists will be different. For the sake of simplicity we assume that within a reasonable range these costs will increase linearly with the dilution of resource. Thus, in our example the costs will be twice as high for the specialists as for the generalist. Other things being equal, we shall expect the abundances of the specialists to be reduced by a factor of 0.5 as compared with the generalist. A summary of the terms involved is provided in Tab. 1. From these terms the expected abundances (N) are obtained as a product of habitat (= resource in this case) range (R), resource dilution (D), and efficiency of the resource use (E) in this habitat:
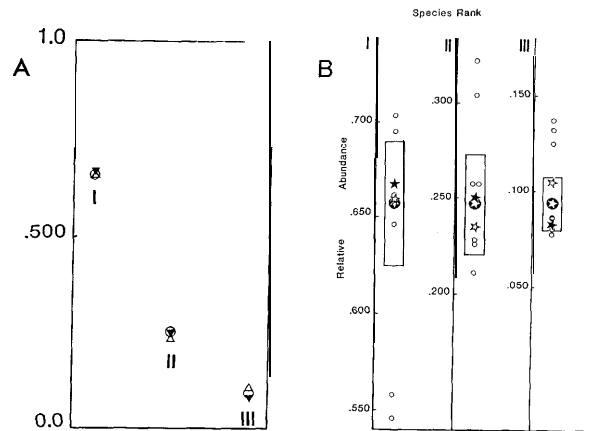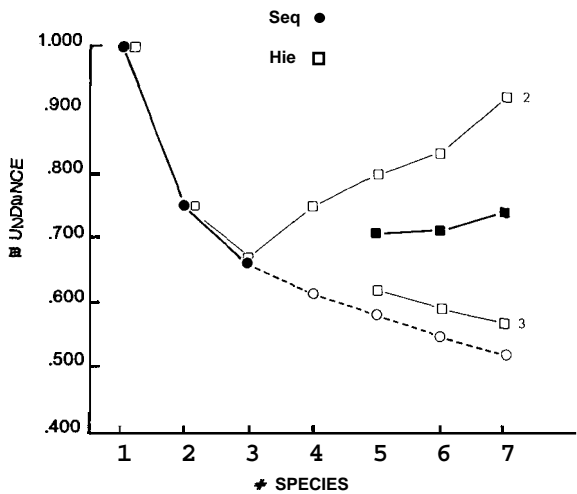

Fig. 3. Comparison of predictions by the Sequential Breakage Model (SBM) and Habitat Based Model (HBM) for a three-species community. Both models are compared with data from natural communities. A – mean values from 90 communities (open circles, see Tab. 2 for sources), predictions of the SBM (open triangles), and by HBM (solid triangles) for the first, second and third-ranking species (I-III, x-axis). Y-axis gives the mean relative abundance. B – the same results enlarged and aligned for the mean relative abundance values from natural communities, with 95% confidence intervals shown (observed data – circles with star, values for individual taxa – small circles, SBM – open stars, HBM – solid stars). The three y-axes are for the first, second and third-ranking species, respectively.

Fig. 4. Comparison of predictions by Sequential Breakage Model (SBM) and Habitat Based Model (HBM) for communities of 1–7 species. In HBM, a five (or more) species community can form when the habitat is subdivided either at two levels (cf. Fig. 2) or at three levels; for example, when one or both of the subunits of the lower level are subdivided again. The number of levels influences the size of possible ecological ranges of species, which results in different predicted abundances. For example, a 7-species community may form with one species at the highest level 1, 2 species at level 2, and 4 species at level 3, or, alternatively, with 6 species at the level 2 and level 3 absent. Results for the I'' ranking species shown only. SBM-circles (open circles – obtained by computer simulation); HBM – squares (open squares – values for a 2 or 3 level community structure; solid squares – average).

$N = R * D * E$ i.e.: $\qquad$ (1)
$G = 1 * 1 * 0.5 = 0.500,$ $\qquad$ and $N = 0.667$
$S1 = 1l2 * 1/2 * 0.75 = 0.1875,$ $\qquad$ and $N = 0.250$
$S2 = 1l2 * 1l2 * 0.25 = 0.0625,$ $\qquad$ and $N = 0.083$

where N is relative abundance (i.e., $N = N/(NG + NS1 + NS2)$. Because both R and D of a species depend on the number of fragments into which the unit of the habitat is subdivided, a more compact and general expression can be derived:

$D = R_i R_t$ $\qquad$ (2)
$R = R_t/R_i$ $\qquad$ (3)

and, substituting for (1):

$$N = \frac{R_i^2}{R_t^2} * E ,$$ $\qquad$ (4)

where R_t is the total range available in the habitat unit in question and R_i is the relative range of ith species.

It should be noted that R and D are not in general identical, but appear so in this example as a result of the assumption of uniform spatial distribution of SU1 and SU2. Nevertheless, the generality of the calculations is

considerable because any expected inequalities between the specialists, that might be due to a different size of the resource, are sufficiently addressed by the assumption of differences in efficiency of resource use. Some of these differences may be viewed **as** due to the differences in resource amount and quality.

The values predicted by the model above can be compared with empirical data. To obtain average relative abundances of species in three-species communities from natural habitats we have pooled the first ranking species, the second ranking species, and the third ranking species. The average values of relative abundances obtained from 90 sets of observed data (Tab. 2) are similar to those calculated from the model (Fig. 3).

The HBM model reacts in a predictable, although not obvious, fashion with the change of habitat heterogeneity. An increase in heterogeneity through additional lower level subdivisions will shift the dominance in favor of the already dominant species. However, an apparent increase in heterogeneity through including more units of habitat will reduce the relative dominance of species. The decrease of heterogeneity will have an opposite effect. In highly heterogeneous habitats the top level may remain partly unoccupied due to absence of a species able to use the whole range of microhabitats. This is probably the case whenever an increase of heterogeneity is associated with the increase of species evenness.

These properties of the model are directly amenable to experimentation. **A** direct test of differences between the **SBM** and **HBM** could be obtained by increasing the relative quantity of resource used by the most specialized species in a controlled three or more species assemblage set up in the hierarchical fashion, as in the flower example. If the **SBM** is correct, the proportion of the top-ranking species should *decrease* with the increase of the quantity of the resource used by 2nd and 3rd ranking species, and the number of species in the assemblage. If the habitat-based model is correct, the relative abundance of the top-ranking spcies should *increase* with the increase of the number of species in the assemblage, provided that additional species colonize lower level subdivisions of the habitat unit. Predictions obtained from the HBM for such assemblages under the assumption of two levels yield much higher values for the first species than the SBM (Fig. 4). A community composed of 5–8 species may be organized in 2 or 3 levels with different predicted relative abundances. Such predictions are again different from the **SBM** and are verifiable by field or experimental data.

Discussion

The sequential partitioning of the resource as suggested by Sugihara (1980) might be acceptable for a specified and narrow array of situations whenever the colonization (also through speciation) of a habitat proceeds from generalists to specialists. We could call this a his-

torical type of dynamics. Yet, for any given and limited pool of species this process ceases eventually to be a significant source of species richness in a community. There is no biological reason then to expect the abundances pattern predicted by the SBM to remain fixed. If this objection **is** correct, then the pattern exhibited by real data needs a different explanation. We believe that the HBM suggests a mechanism constantly operating, thus different from the unique sequence of events required by the sequential model. The unequal use of resources in a habitat unit is a result of its hierarchy only and does not require differences between species other than specialization to different habitat components. The HBM implies that generalist and specialist species living in the same habitat experience different constraints resulting from the hierarchy of the environment which effectively reduces the abundances of specialists. According to HBM, the hierarchy of the environment is sufficient to explain the pattern of species abundances, but there are other differences among the species that may generate at least qualitatively similar patterns. Notably, differences in body size and trophic position have been associated with abundances. The role of differences in body size and trophic position will probably increase with a decrease in ecological similarity of species in a collection. Neither model, however, aspires to address the patterns in collections of species from different trophic levels, or including body sizes different by an order of magnitude that would be required to explain considerable differences in their abundances.

Finally, our model is a considerable simplification. Further research needs to explore rules linking abundances of species to resource use and the role factors influencing that relationship. These factors may include specification of conditions under which an equilibrium between resources and densities is observed, e.g. spatial and temporal scale considerations, or modifiers such as body size, trophic position, quality of food, and foraging strategy. We envision that these and similar considerations can be appended to our basic model.

Brief comparison between the models

Habitat-based model	*Sequential breakage*
Biological motivation	Formal motivation
n breakage at each step	Sequential bifurcations
Good predictions for for three species	Good predictions for for three species
Sensitive to environmental heterogeneity	Unrelated to environmental heterogeneity

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