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Species Richness and Population Dynamics of Animal Assemblages. Patterns in Body Size: Abundance Space

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Species richness and population dynamics of animal assemblages. Patterns in body size: abundance space

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SUMMARY

Links between population dynamics, the relative abundance of species and the richness of animal communities are reviewed within the framework of a simple conceptual model, based on body size and abundance. Populations of individual species occupy positions in this body size: abundance space. Problems of relative abundance and absolute species-richness revolve around a number of simple questions, including: what determines the upper and lower bounds (maximum and minimum population densities) of species in the assemblage; what determines the overall density of points (number of species) within these bounds; and how are the vertical and horizontal partitioning rules between species decided? The answers to these, and related questions, are briefly reviewed.

1. INTRODUCTION

A simple conceptual model based on body size and abundance links population dynamics with the richness and relative abundance of animal species within a local community (figure 1). Although it is simple, it allows us to bring together and explore a wide variety of processes hitherto considered largely in isolation. Each point in figure 1 represents the average abundance and average body size of a species in the assemblage. Fluctuations in density and changes in body size are a complication dealt with briefly towards the end of this paper. The model is simplest to interpret when applied to species from one trophic level, although data are too restricted for this ideal to be fully realized at the moment. It seems unlikely that the model can be usefully applied to animals with modular growth, such as corals or bryozoans.

If data are collated for animal populations from a wide variety of published studies across many communities and ecosystems, average population densities tend to be inversely correlated with body size (Peters & Wassenberg 1983; Damuth 1987). In contrast, collections of organisms from within local assemblages reveal the more complex shape shown in figure 2 and idealized in figure 1 (Lawton (1989)) and references therein; Blackburn *et al.* 1990), as do data for primates in different habitats (Clutton-Brock & Harvey 1977) and birds throughout the North American continent (Brown & Maurer 1987). This pattern is remarkably consistent across a wide range of taxa, habitats and geographic areas. Possible reasons for the differences between data assembled by Damuth (1987) and by Peters & Wassenberg (1983), and these more taxonomically and geographically restricted studies are discussed in Lawton (1989) and Blackburn *et al.* (1990).

This paper takes the pattern summarized in figure 1 as the norm and asks three questions.

(i) What determines maximum average abundances for species in the assemblage, i.e. what determines the slope and amplitude of the upper-bound *A–B*?

(ii) Below some critical density, *C–D*, species become so rare that they disappear from the community. What determines minimum viable population densities?

(iii) How is the density of points within body size: abundance space determined? This problem embraces at least two, interrelated subquestions, namely what are the horizontal and vertical partitioning rules that determine the positions and numbers of data points within the defined bounds?

Two details about figure 1 are not considered here. The first is the range of body sizes (*E–F*) from the smallest to the largest species in the assemblage. In its more interesting form, this range will be set by evolutionary design constraints; less interestingly, it will have been set arbitrarily by the investigator. Neither is a question of population regulation or

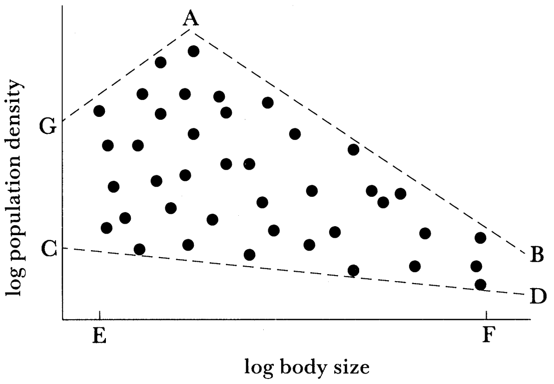

Figure 1. Generalized relation between body size and population density for animals in a local assemblage. Each dot represents the average body size and abundance of a single species in the assemblage. The limits (*A–B*, *E–F* etc.) are discussed in the text.

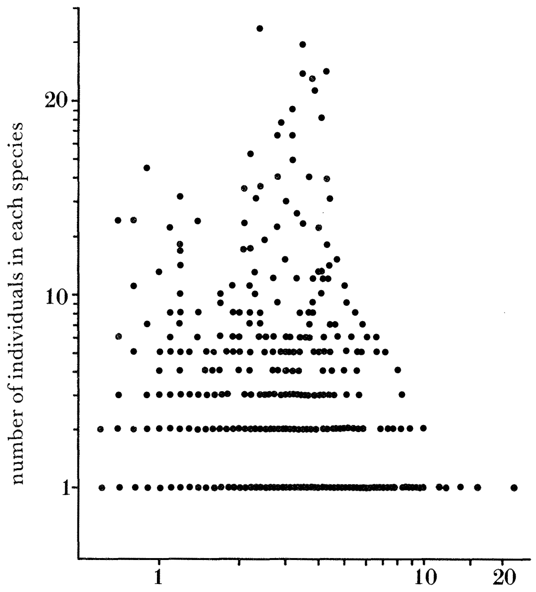

Figure 2. Data on 859 species of adult beetles plotted in body size: abundance space. The beetles were collected in single insecticide foggings from the canopies of ten Bornean lowland rainforest trees (Morse *et al.* 1988). Unlike the hypothetical data in the preceding figure, the lower bound (*C–D* in figure 1) is horizontal, because large numbers of species are represented by single individuals in the collection. It is not clear how many of these single individuals are 'tourists' without established local populations, or how the shape of the lower bound might be altered by making much larger, or sequential collections in an attempt to distinguish statistical sampling effects from biological ones.

dynamics. Second, there is a small region *G–A* where the upper bound declines as average body sizes decline. This small region is not well understood, although it is present in all the body size: abundance plots for local assemblages that I have seen. It may simply be a sampling phenomenon (Blackburn *et al.* 1990), or it may be something more interesting (see Brown & Maurer (1987, 1989) for further discussion).

2. MAXIMUM POPULATION DENSITIES AND BODY SIZE

Species whose populations lie along, or close to the upper bound (*A–B*) of figure 1 are, by definition, the most abundant in the assemblage. Being the most abundant, it seems reasonable to suppose that they are resource limited. If so, the predicted slope of the line *A–B* depends on average resource use. For many animals, individual metabolic rates, and hence food requirements scale as $W^{0.75}$ (Peters 1983), where W is body mass. Other things being equal (not least the total availability of food for animals of different body sizes), maximum population densities will therefore scale as $W^{-0.75}$. Similar arguments can be developed for species that are limited by the space or volume of the habitat (see, for example, Duarte *et al.* (1987)), or by territoriality (Schoener 1968; Clutton-Brock & Harvey 1977).

Discovering whether the upper bound in a diagram such as figure 1 conforms to or departs from theoretical expectations presents statistical difficulties, and I know of no formal attempts to carry out such a test; less formal inspection reveals an upper bound for birds in Brown & Maurer (1987) that is close to -0.75 (J. H. Brown, personal communication). Slopes of log body size: log abundance plots compiled from the literature, for species from a wide variety of different communities sometimes also lie close to -0.75 (Damuth 1987), which is to be expected if such data are biased towards the commonest species. But other studies report slopes that are clearly not -0.75 (Peters & Wassenberg 1983; Peters & Raelson 1984; Brown & Maurer 1986), perhaps reflecting the efficiency with which rarer species have been included in the surveys (Brown & Maurer 1986; Lawton 1989), as well as different ways of grouping species before analysis.

Surprisingly, even less is known about the magnitude of the upper bound. It seems reasonable to suppose that *A–B* will be higher in more productive ecosystems, but I know of no explicit test of this hypothesis. I return to the question of the magnitude of the upper bound in a later section.

3. MINIMUM VIABLE POPULATION DENSITIES

Defining the lower bound, *C–D*, in figure 1 is difficult for two reasons, one practical, the other conceptual. Practically, rare populations are by their nature difficult to study. Conceptually, the lower bound is elusive because many of the rare species taken in samples of a community may be transients; there is a continuum from vagrants, through species that occasionally breed in the community, to rare but permanent members with self-sustaining populations (see legend to figure 2); and the position of species along this continuum will depend on the size of the area being investigated. Nevertheless, it is worth considering what we know about the determinants of minimum viable population densities, at least in principle. The tentative suggestion in figure 1 is that minimum viable densities are higher for small-bodied species (Lawton (1989); see also arguments in Brown & Maurer (1987)). This suggestion hinges on two lines of reasoning.

First, species that are rare locally (i.e. those species whose populations lie towards the lower bound of figure 1) tend also to have restricted geographical distributions (Brown 1984; Gaston & Lawton 1988*a*, *b*). In other words, they have small total population sizes. Second, although the data are much poorer and more difficult to interpret than is generally realized (McArdle *et al.* 1990) populations of small-bodied species may fluctuate more on average than populations of large-bodied species (scaled for generation time) (reviews in Gaston & Lawton (1988*a*, *b*); Hanski, this symposium). If they are real, these differences probably reflect the greater vulnerability of smaller organisms to density independent disturbances. Since fluctuations can drive rare populations extinct, minimum viable total population sizes should therefore be larger for small-bodied species, and large-bodied species should be able to maintain themselves in communities at lower overall densities.

A counter argument runs as follows. Although populations of rare, small-bodied species are more vulnerable to environmentally driven stochastic extinctions than similar sized populations of large-bodied species, small-bodied species have an advantage in higher intrinsic rates of increase (Gaston & Lawton 1988*a*, *b*; Pimm *et al.* 1988; Lawton 1989). Higher intrinsic rates of increase carry rare populations out of the 'danger zone' faster, and may favour the persistence of small-bodied species at lower average total population sizes and densities than are sustainable by large-bodied species.

Evidence can be adduced for both arguments (see Lawton (1989) and Pimm *et al.* (1988) for detailed discussions). For example, below a total population size of about seven pairs, large-bodied species of resident birds on British islands are less prone to extinction than are small-bodied species. Above seven pairs, these differences disappear and may possibly be reversed (Pimm *et al.* 1988). The implication is that both intrinsic rates of increase and vulnerability to environmental stochasticity play a part in determining minimum viable population sizes and densities. Additional complexities centre on the fact that not all low-density populations have restricted distributions (Rabinowitz *et al.* 1986; Gaston & Lawton 1990*a*, *b*), severing the theoretical link between determinants of minimum viable population sizes and minimum viable densities.

In brief, we have only the haziest notion how the lower bound in figure 1 is determined. My suspicion is that usually the bound slopes up as species get smaller, but I have no great confidence in the prediction. It already appears to be refuted by birds sampled throughout North America (Brown & Maurer 1987), albeit these are not data from a local community.

4. THE DENSITY OF POINTS IN BODY SIZE: ABUNDANCE SPACE

Total species richness in a community is a product of the bounds on figure 1, and the density of points within these bounds. A great deal of experimental and theoretical work in population dynamics and community ecology has been concerned with discovering how the density of points is determined, and whether there are, or are not, hard limits to the number of species that can be packed into a particular space.

(*a*) *The role of regional processes*

Work on the richness of local assemblages has focused on species interactions. Much less attention has been paid to the influence of regional (biogeographic) processes. Yet the latter are central to an understanding of local community diversity. The theory of island biogeography (MacArthur & Wilson 1967) tells us that at equilibrium, small or isolated patches of habitat hold fewer species from a regional pool than large, near patches. Individual species may be missing entirely from suitable, but isolated habitats (Harrison *et al.* 1988; Lawton & Woodroffe 1990). It is unclear whether species occupying different regions in body size: abundance space are differentially influenced by isolation. For instance, species that are common in the regional pool may generate more colonizing propagules. Body size ought also to influence dispersal abilities (Gaston & Lawton 1988*a*, *b*), although effects may be complex, not least because very small body sizes may facilitate passive dispersal and large body sizes may aid directed movements.

Familiar as these ideas are, ecologists have been slow to work out the contribution of regional processes to local diversity. Yet patterns of invasion, speciation and extinction over evolutionary time make an enormous difference to the size of the regional pool of species from which local communities are assembled (for a particularly illuminating example, see Pearson & Ghorpade (1989); for a general discussion of the problem, see Ricklefs (1987). A much neglected question is the relation between the number of species in the regional pool of potential colonists, and the richness of local assemblages (Lawton 1982; Cornell 1985*a*, *b*). There are three possibilities (figure 3*a*): all (model 1), or a constant proportion (model 2), of the species in the regional pool occur locally; or (model 3), there are constraints on the number of species able to coexist locally.

For insect herbivores on oak trees (Cornell 1985*a*, *b*) and on bracken fern (Lawton 1982, 1990; Compton *et al.* 1989; see figure 3*b*) the number of species living together locally is a roughly constant proportion of the number of species in the regional pool from which these communities are assembled (figure 3*a*, model 2). There is no evidence that the number of species is constrained in the manner envisaged by model 3. Vacant niches (unused resources that are utilized in other assemblages) are easy to identify, and there are no signs of density compensation in sparse species assemblages (see, for example, Lawton 1982). It is unclear what proportion of ecological assemblages conform to model 2; for those that do, understanding local (within community) constraints on the density of points in body size: abundance space is not very interesting. The answers lie elsewhere, in history and regional biogeography.

Model 3 communities present the other extreme, and certainly exist (Terborgh & Faaborg 1980), although how common they are is again uncertain. In model 3 communities, numbers of coexisting species are constrained; a veritable library of ecological literature has been devoted to discovering how.

(*b*) *Constraints on numbers of coexisting species: horizontal partitioning rules*

The number of coexisting species may be constrained by interspecific competition for resources such as food or space (which has been very well studied) or by 'apparent competition' for 'enemy-free space' (far less well studied) (Holt 1977, 1987; Jeffries & Lawton 1984; Lawton 1986). These constraints may have little or nothing to do with body size (Chesson, this symposium; Shorrocks & Rosewell 1986), or they may be strongly influenced by it. Here I want to focus

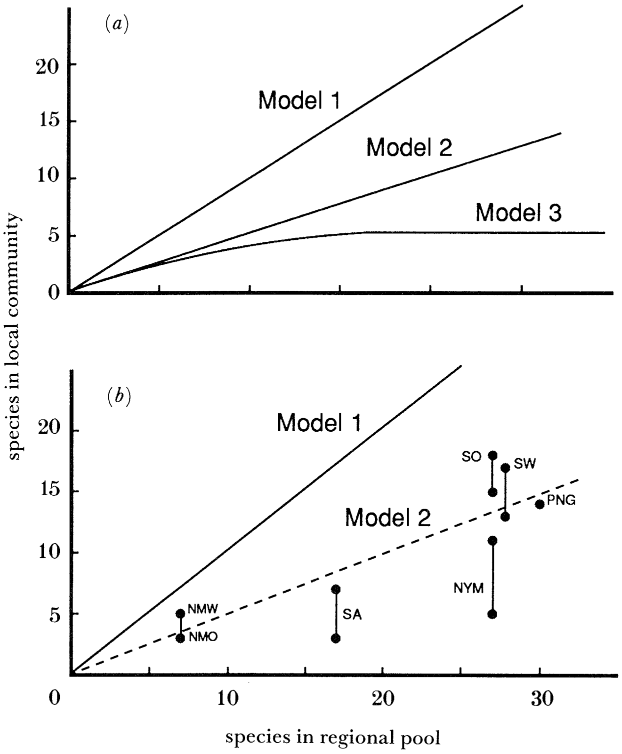

Figure 3. (*a*) Theoretical relations between regional and local species richness in ecological systems (Cornell 1985*a*, *b*). Model 1, all species in the regional pool are found in every community; Model 2, proportional sampling; Model 3, local communities saturate with species. (*b*) Relation between local and regional species richness of herbivorous arthropods (insects and mites) feeding on bracken in different parts of the world (Lawton 1982; Lawton & Gaston 1989; Compton *et al.* (1989) and references therein). Maximum and minimum values for local communities are shown for each study area. The dotted line for model 2 is for proportional sampling in which half the species in the regional pool are found locally (it is not a fitted line). (NMO, NMW, New Mexico open and woodland areas; SA, South Africa; NYM, North York Moors; SO, SW, Skipwith (York) open and woodland areas; PNG, Papua New Guinea.)

briefly on constraints on the number of coexisting species that are influenced by body size; that is, I want to examine the horizontal partitioning rules in figure 1.

The notion that there may be limits to similarity in the body sizes of competing species is usually attributed to Hutchinson (1959), although he acknowledges Julian Huxley as the originator of the idea (see Carothers 1986). Thirty years later, progress has been frustratingly slow. Schoener (1986, 1989) provides two excellent overviews. Theory based on various kinds of abstract models is equivocal on whether there are, or are not, hard limits to niche overlap (Abrams 1983). Hutchinson's much cited (albeit originally highly tentative) observation that body-length ratios of the larger to the smaller species are typically of order 1.3 may be a consequence of 'sampling' from a log-normal distribution of body sizes with small variance (Eadie *et al.* 1987). And there are still rather few convincing studies linking the observation that species are less similar in body size than expected by chance (see, for example, Schoener (1984); Diamond (1986)) with detailed studies on the mechanisms of the competitive process (Juliano & Lawton 1990*b*); Darwin's finches continue to inspire and lead our understanding (Grant 1986).

In an attempt to clarify relations between body size, limiting similarity and competitive mechanisms, Juliano & Lawton (1990*a*, *b*) examined guilds of hydroporine and laccophiline water beetles (family Dytiscidae) in habitats near York in northern England. The adults are small (largest species *ca.* 5.5 mm long), long lived, and predatory; assemblages typically contain several species that differ in body size and shape. Body size and preferred prey size are highly correlated. We compared the body size and shape of species in real assemblages with random draws from the pool of species present in the area, and with assemblages of 'pseudospecies' drawn from random points in the full range of morphological space; analyses were performed by using all the species recorded in each assemblage, or excluding rare species (defined in a standard way).

Two natural assemblages from large, well-buffered water bodies containing predatory fish were more regularly and widely spread out in morphological space than expected by chance, and these patterns were stronger when comparing just abundant species with randomly assembled 'pseudospecies'. There are theoretical reasons to expect that non-random distributions of species in body size: abundance space will be easier to detect under both these circumstances (see Juliano & Lawton (1990*a*) for further discussion). In contrast, sets of species from seven small, acid pools without fish were randomly distributed in morphological space. Armed with these results, we predicted that species in the non-random assemblages would compete for food in the manner envisaged by Hutchinson (1959), and that the random assemblages would not. Unexpectedly (Juliano & Lawton 1990*b*), we could find no evidence that adults in the two non-random assemblages competed for food, or that intensity of competition was related to differences in adult body size. In this respect, they appeared identical to the assemblages in which adults were randomly assembled in morphological space.

These results epitomize the problems that have confronted attempts to discover simple, general principles governing the horizontal partitioning rules in body size: abundance space. Pessimists would argue that ecologists have made essentially no progress with the problem in over thirty years. My view is that we have made reasonable progress with a hard problem. We now know that the question of competition and hard limits to species overlap are irrelevant for some systems. For other systems, competition is clearly important, and a series of empirical observations, experiments and models suggest that sometimes competition translates into limits on similarity in body size, and sometimes it does not. On other occasions, as in the water beetles, non-random patterns in morphology do not seem to be a result of competition for food, in the manner envisaged by Hutchinson; what the mechanism is in this particular case remains obscure. It may involve size-selective predation by fish, but we have no firm evidence on this point.

As is so often the case in ecology, theory and explanations are contingent, not absolute (Schoener 1986). The challenge now is to develop a better understanding of the contingent, horizontal partitioning rules, both in theory and in practice, building upon the rich body of data and models that already exist.

(*c*) *The vertical partitioning rules in theory*

It is clearly artificial to treat the horizontal and vertical partitioning rules as distinct, or to separate either from competitive processes that set limits to the number of coexisting species independently of body size. Interspecific competition depresses population densities on figure 1 and competitive exclusion happens when densities cross the lower bound *C–D*. Nevertheless, it is conceptually useful, for present purposes, to discuss the two sets of rules separately.

To ask about the relative abundance of species is, by definition, to ask about the vertical partitioning rules in figure 1. I am not aware that anybody has worked out in detail for more than two or three species within one trophic level why some species in a community are common and others are rare. The common species, close to the upper bound, are presumably resource limited, competitive dominants. There are several reasons why other species in the assemblage may be rarer than this, including: specializing on rare resources (small fundamental niches); competitive inferiority (realized niches much smaller than fundamental niches); the impact of natural enemies or diseases (q, in the sense of Beddington *et al.* (1978), $\ll 1$); and frequent, density-independent disturbances. It would be interesting to map out the reasons for commonness and rarity in particular species assemblages.

Although detailed information is lacking on why some species are common and others rare, even in well studied communities, we do know that despite population fluctuations around long-term averages, in assemblages where the problem has been looked at, the common species generally stay common and the rare species stay rare; that is rank abundances are statistically significantly correlated over time (Lawton & Gaston (1989) and references therein; Owen & Gilbert 1989). An alternative model of community dynamics, the 'core-satellite hypothesis' (Hanski 1982), predicts that species within assemblages switch haphazardly from common to rare or absent and back again. I know of no animal communities where this model has been verified in detail (Gaston & Lawton 1989). However, there is growing theoretical and empirical evidence that certain assemblages can exist in alternative stable states in identical physical environments, particularly where habitat fragmentation isolates the alternative states (Robinson & Dickerson 1987; Barkai & McQuaid 1988; Moss 1989; Polis *et al.* 1989; Sinclair 1989). Alternative stable states imply that species occupy alternative equilibrium positions measured on the y-axis of figure 1.

Given the rich variety of possible dynamics that exist at any points in body size: abundance space, it seems unlikely that a single model could describe the vertical partitioning rules, for species lying within a particular range of body sizes. Yet a model based on 'sequential niche breakage' (Sugihara 1980) comes intriguingly close. It may work because it stands back from the details. As Sugihara points out (p. 773): 'it is plausible to consider apportionment in a heterogeneous resource pool, involving the subdivision of several different sets of niche axes. This allows the apportionment analogy to be extended to large species ensembles which do not possess a uniform set of governing factors'.

Sugihara envisages communal niche space as a 'unit mass', sequentially split up by the component species, so that each fragment denotes relative species abundance. The initial unit mass is broken to produce two fragments; one of these is then chosen randomly and broken to yield a third, and so on. The rules for determining apportionment of niche space (the size of the fragments) between two species at any particular break are discussed by Sugihara (1980). Applying these rules, and extending the breakage sequence to a large number of species results in a distribution of fragment-lengths (species abundances) that is canonical log-normal. In other words, the theoretical species–frequency distribution generated by this minimal model is exactly the distribution of species' abundances observed in many communities, although by no means all (exceptions are reviewed by Preston (1980); Ugland & Gray (1982); Harmsen (1983); Wright (1988)).

Not unexpectedly, Sugihara's model has attracted a good deal of attention (see, for example, Ugland & Gray (1982); Harvey & Godfray (1987); Pagel *et al.* (1991) and has spawned a number of related studies (Kolasa & Strayer 1988; Kolasa 1989; Glasser 1989) exploring alternative models of niche breakage and resource partitioning between species, with no sign, as yet, of an emerging consensus. Three things, do, however, seem obvious. First, given that not all communities have the same underlying species-frequency distribution (log-normal, log-series or something else), it is very unlikely that one model will be adequate to explain species' relative abundances in all systems; once again, we need contingent theory. Secondly, we need to think very hard why minimal, phenomenological models work at all; in particular, it would seem sensible to try to derive the general partitioning rules from detailed models that explore the full range of dynamic processes known to be operating at different points in body size: abundance space (see above). Hughes (1986) has made an important start in this direction.

Thirdly, most existing models ignore body size (Harvey & Godfray (1987); Pagel *et al.* (1990) provide important exceptions). Species–frequency distributions are usually fitted to groups of similar species, moths at a light trap, for example. Although these will usually cover a limited range of body sizes, there may be sufficient differences between the largest and smallest species in the assemblage to make detection of the underlying patterns and mechanisms difficult. The way in which log-normal distributions of species' abundances are built up by combining data from species of different body sizes, incorporating figure 1, is explained in Morse *et al.* (1988).

It is unclear what range of body sizes can and should be grouped together in studies of species–frequency distributions, but suppose that figure 1 can be divided into *n* vertical strips of appropriate width, in which the largest species in each strip is *l* times the mass of the smallest. Suppose also, for the sake of argument, that the real species-frequency distribution within each strip is a log-series. If we now view the system through a cruder lens, say by combining triplets of strips (such that the largest species have l^3 the mass of the smallest) the underlying species frequency distribution in the wider strip may appear to be roughly log-normal, rather than a log-series, because combining log-series distributions is one way to generate a log-normal curve. In other words, a good deal more thought needs to be given to the way in which species of different body sizes are grouped together in empirical studies of resource partitioning and species frequency.

(*d*) *The vertical partitioning rules for North American birds*

The most important practical contribution in this genre is an analysis of biomass and energy use during the breeding season for 380 species of terrestrial birds across the whole of North America north of Mexico (Maurer & Brown 1988). Although Maurer & Brown seek continental-wide patterns, their findings may reflect what happens within smaller areas; and even if such patterns are different, the study points the way to the kinds of analyses that need doing within local assemblages. Their study combines species from different trophic levels; ideally, future work should distinguish between trophic groups.

Species were assigned to arbitrarily defined logarithmic mass classes ($n = 9$, $l = ca.\ 2$). Knowing average breeding densities for each species, Maurer & Brown (1988) could then work out patterns of energy use by each species within these nine size bands. As species within a band are approximately the same size, relative energy use is approximately the same as relative abundance within each size category (notice this is not the case when species of very different body sizes are being compared, because population energy use scales as $(\text{body mass})^{0.75}$).

In the present context, Maurer & Brown's three most important results are: (i) within each size class, population energy usages (and hence species' relative abundances) fit a log-series; (ii) the most abundant species in each size band uses the same fraction (*ca.* 10%) of the total energy used by all species in that size band; (iii) the density of species is higher in the small mass-classes; that is, resources are more finely divided, and species are more tightly packed in body size: abundance space toward the left-hand end of the ordinate in figure 1.

This last point is important, because it implies that parameters defining the exact ways in which species divide up resources are not identical for all body sizes (although the qualitative rules appear to be the same). The second point is important if we are to understand how productivity influences the upper bound in figure 1, and is dealt with briefly in the next section. The first result apparently conflicts with Sugihara's (1980) attempt to model the vertical partitioning rules as a log-normal distribution. The mismatch may, however be more apparent than real, partly because a relatively small sample of species from the right-hand tail of a log-normal distribution may look like a log-series, and partly because, as we have seen, pooling log-series may generate a log-normal distribution!

It is probably not helpful to pursue these more detailed points, mainly because the scale of Maurer & Brown's work (the avifauna of a whole continent) may, in the end, be ill-suited to studies of local communities. I have no doubt, however, that their work shows the types of data we need to gather for local species assemblages, and together with the general models of Sugihara and others, points the way towards a clearer understanding the vertical partitioning rules, and how communities are assembled in body-size: abundance space.

5. PRODUCTIVITY AND SPECIES RICHNESS

I want, now, to return briefly to the problem of the upper bound, and the relation between it, and overall species richness.

As MacArthur (1972) anticipated and Wright (1983) formalized, a number of studies have now shown geographical patterns of increasing species richness with increasing energy availability or habitat productivity (Brown 1975; Brown & Davidson 1977; Currie & Paquin 1987; Turner *et al.* 1987; Turner *et al.* 1988; Adams & Woodward 1989; Currie 1990). These results can be interpreted in terms of figure 1, via links between primary productivity and total consumer biomass.

The biomass of primary consumers increases roughly as the 1.5 power of net primary production in terrestrial ecosystems (McNaughton *et al.* 1989). It is not surprising that more energy entering the system results in a larger lump of animal biomass to be partitioned among species; it is less obvious why this increase in biomass is a power function of net primary production. It is this total biomass of animals that Sugihara's and related models seek to partition among species.

As has already been observed, Maurer & Brown (1989) find that the most abundant species in each body-size category use about the same fraction of the total energy used by all species. If these arguments extend to systems of different overall productivities (and their data for different regions of North America suggest that they do) it implies that the upper bound in figure 1 will rise as overall productivity rises, with the commonest species taking an approximately constant percentage of total resources available for species in that body-size range. It is then more or less inevitable that more productive systems will contain more species if partitioning of remaining resources stops when the rarest species in the resulting assemblage reaches the critical lower bound, *C–D*, in figure 1. Indeed, because the total lump of herbivore biomass to be divided up rises as the 1.5 power of net primary production, the scope for adding rare species increases quite dramatically as productivity rises, particularly if the partitioning rules are a log-series, or something similar. Interestingly, the essence of this idea is explicit in Hutchinson (1959). He wrote (p. 150): 'If the fundamental productivity of an area is limited... to such a degree that the total biomass is less than under more favourable conditions, then the rarer species in a community may be so rare that they do not exist'. This seems to me to be at least as interesting an idea as the much cited rule for limiting similarity between species and yet has received only a fraction of the attention.

6. CONCLUDING REMARKS

(*a*) *Variations in size and density*

It is clearly a gross oversimplification to treat the points representing individual species in figure 1 as average values. Real species fluctuate in density and many (e.g. fish) change markedly in size during independent life in the wild. It is unclear whether an emerging synthesis of the way in which species are assembled into communities will have to deal with these inevitable complications, or whether average values will do. The answer may depend on the taxa and upon the magnitude of population fluctuations. Changes in body size can probably be ignored in assemblages of adult birds or water beetles; they almost certainly cannot be ignored for fish, which change positions in interesting ways in body size: abundance space as they mature (Gaston & Lawton 1990*b*). Likewise, if populations display chaotic or cyclic dynamics in species-rich assemblages (Godfray & Blythe, this symposium; Sugihara & Grenfell, this symposium), it may be impossible to ignore the fluctuations as we try to understand community assembly 'from the bottom up'. My own view is that we need to keep these complexities firmly in view in the middle distance, and concentrate our immediate attention on average densities and body sizes. The problems posed by this limited perspective are already quite complicated enough.

(*b*) *Synthesis*

The full range of population dynamic processes concatenated into figure 1, and which are therefore involved in determining the relative and absolute species richness of animal assemblages, make it impossible to build a comprehensive, realistic and reasonably detailed model of local community structure. That is not the point of summarizing the processes involved. Rather, the aim of the present paper has been to draw attention to neglected details that form part of the whole picture, and that can be resolved by a combination of observations, models and experiments; examples include the 'lower bound' problem, links between local and regional species richness, and the question of how best to construct detail-independent models of the vertical partitioning rules. I view figure 1 as a framework for organizing and cataloguing our thoughts; without it, or something similar, community ecologists are in danger of failing to see the wood for the trees, and hence failing to see how microscopic theories and processes contribute to macroscopic patterns that appear, in the end, to be both simple, and general.

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