Chapter 5

Breaking the stick in space: of niche models, metacommunities and patterns in the relative abundance of species

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Introduction

> *'The available evidence apparently does suggest that a great many biological "universes" have the logarithmically-Gaussian form . . . If birds in a valley, moths in a trap, plants in a quadrat, insects in a sweep net, and micro-organisms in a suspension of hay do in fact all agree in this, it would seem that some very general law must lie behind it all.' (Preston 1948)*

The search for general laws underlying the structure and functioning of ecological systems has been a long-term goal for ecology. This search, which started with the early detection of general patterns in the diversity, distribution and abundance of species, has fructified in recent years as a consequence of the establishment of the macroecological research programme within ecology (Brown 1995, 1999; Maurer 1999; Gaston & Blackburn 2000; Marquet 2002) and because of the emergence of the science of complex systems (e.g. Waldrop 1992; Cowan *et al.* 1994; Levin 1999). At the core of both macroecology and complex-system science is the search for generalities in the form of power-law behaviour and scale invariance in patterns, such as the distribution of city sizes, body sizes, words in natural languages, abundance within natural communities (e.g. Marquet *et al.* 1990; Schroeder 1991), the growth of firms, countries or natural populations (e.g. Keitt & Stanley 1998; Stanley *et al.* 2000). However, the discovery of patterns and their statistical description is the beginning of a process that ends with the proposition of hypotheses about mechanisms that potentially could give rise to the observed phenomena. The history of ecology tells us that the time it takes to traverse this path is usually very long and is marked by bursts of activity reflected in the generation and coexistence of several alternative models and hypotheses that can explain the same phenomenon. Although this is true for most macroecological patterns (e.g. Gaston & Blackburn 1999), it is paradigmatic in the case of those related to the commonness and rarity of species (see Fig. 5.1).

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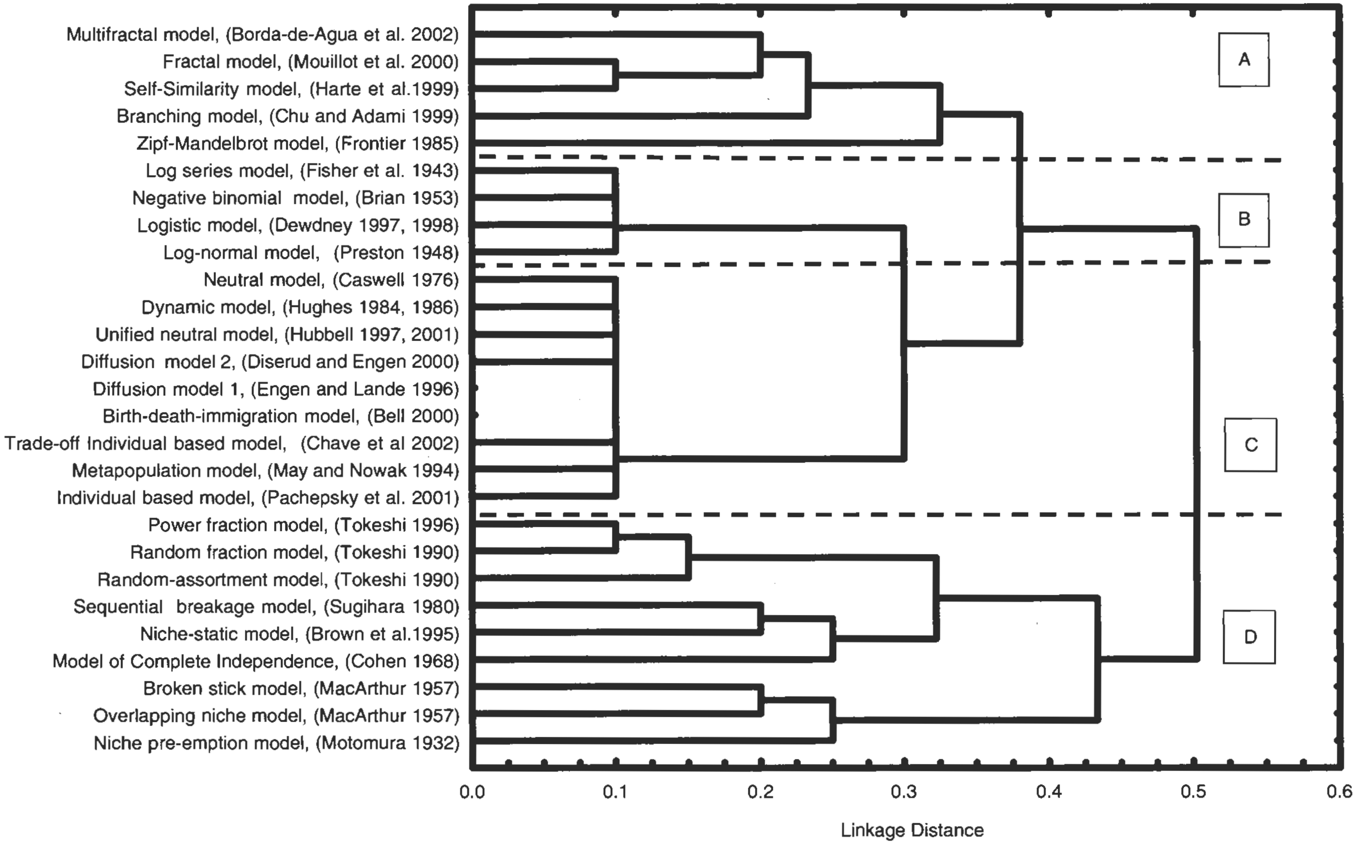

Figure 5.1 Models proposed to explain patterns in the relative abundance of species. For the purpose of graphical representation we carried out a cluster analysis using the UPGMA algorithm and the percentage disagreement distance metric. To construct the distance matrix, models were classified according to the inclusion (1) or not (0) of different features: metacommunity dynamics, birth–death processes, speciation process, niche apportionment processes, ecological equivalency, spatially implicit, spatially explicit, phenomenological, fractal theory and year of publication (scaled to 1). Cluster A groups models based on fractal processes or theory, B identifies statistical models, C groups dynamic models based on birth–death processes and D groups niche-based models (see text for discussion).

In this chapter, we attempt to show part of the scientific history underlying patterns in the distribution and abundance of species, and its place within the macroecological research programme, with emphasis on a particular class of explanations based on niche apportionment mechanisms, generally known as niche models. We will characterize these models, show that their key assumption that the apportionment of resources and individuals are equivalent processes holds, and finally take niche apportionment models one step further by making them spatial, stochastic and dynamic, and mechanistically linked to species life-history attributes. We do not expect to provide a final answer for the empirical reality we address; our aim is to contribute with a valid alternative explanation that potentially could serve this purpose. Foremost, however, our effort should be understood as an attempt to unify niche models with models based on birth–death processes (e.g. Hubbell 1997, 2001; Bell 2000). We do this by connecting resource acquisition with reproductive output in a spatially explicit metacommunity model. We conclude that niche models provide a valid framework to understand patterns in the distribution of abundance.

The pattern at issue

For more than 60 years it has been recognized that species are not equally abundant in samples from local communities. The existence of regularities in the distribution of abundance prompted the development of several models that supposedly captured the pattern. Among them, those that have received most attention probably are Fisher's log-series model (Fisher *et al.* 1943) and Preston's log-normal model (Preston 1948), especially in its canonical form (Preston 1962), but there are several others (see Fig. 5.1). Fisher's sampling model was based on the assumption that the true distribution of abundance was a gamma distribution (Fisher *et al.* 1943; Brian 1953; Kempton & Taylor 1974), whereas the sample distribution of individual abundances was a Poisson series, such that the compound distribution was a negative binomial, which in the infinite limit gave rise to a simple model to predict the expected number of species with *n* individuals, known as the log-series. Under this model rare species with one individual (singletons) are the most abundant (Fig. 5.2b). Preston (1948, 1958) on the other hand assumed that the true distribution of abundance or 'universe' was log-normal, and showed that by graphing species abundance in classes of doubling number of individuals (called octaves), the resulting distribution of abundance in samples was humped with few rare and common species and many species of intermediate abundance (Fig. 5.2a). Interestingly, although Preston's universe was log-normal, samples in local communities were not. Preston (1948) noticed that the sample will tend to look like the hypothetical universe with the left-hand end missing, or veiled, because of the underrepresentation of very rare species in small samples (which he suggested will resemble a log-series on an arithmetic scale). This implies that as the sample gets larger the distribution or universe will be progressively unveiled and eventually will become log-normal. Preston's (1958) analysis of the Audubon Christmas counts and Williams' (1953) analysis of British birds partially confirm this prediction (see also Whittaker 1965).

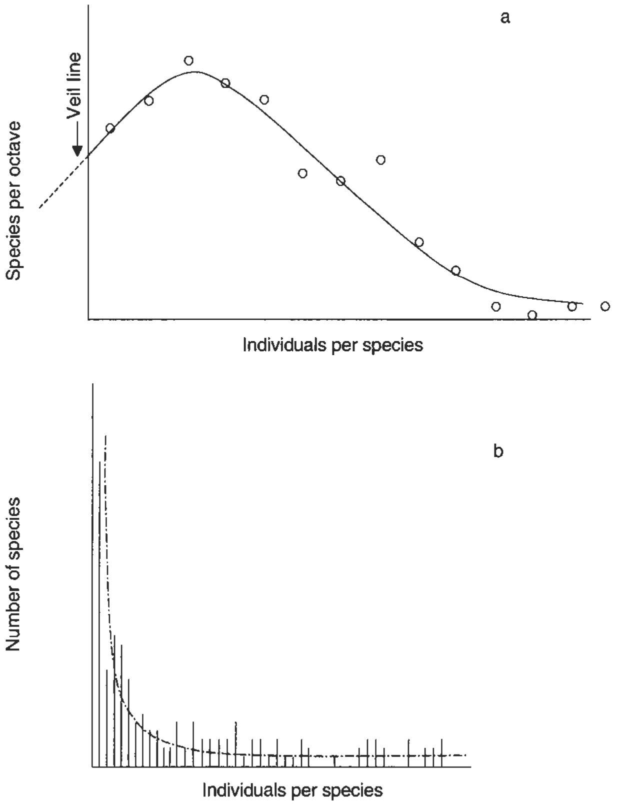

Figure 5.2 Illustration of (a) Preston's log-normal model fitted to data on moths caught in light traps (after Preston 1948) and (b) Fisher's log-series model fitted to data on Rothamsted's Lepidoptera surveys (after Fisher *et al.* 1943).

Fisher's and Preston's models can be dubbed as phenomenological or inductive (e.g. Hubbell 1997, 2001) as they lack any explicit reference to generating mechanisms, although some have been proposed (e.g. Kendall 1948; MacArthur 1960; May 1975; Caswell 1976). Further, the statistical assessment of the fit provided by the log-series and log-normal models to different data sets has produced mixed results (e.g. Hughes 1986; Magurran 1988). However, beyond these problems is the critical issue about the assumptions they make regarding their derivation and in particular on the nature of the parent distribution or universe from where samples were taken. Both Fisher and Preston assumed that the universe corresponded to a humped distribution with either a zero (log-normal) or positive skew (gamma). Only recently have high-quality data on the abundance of species at large spatial scales become available, mostly for birds in North America, Britain and other European countries. This has allowed the possibility to access the 'universes' that Preston and Fisher assumed in their models. One of the first analyses of this issue was carried out by Nee *et al.* (1991a). These authors, using data on the abundance of British birds, reported that Preston's unveiled distribution was not log-normal but distinctly and significantly left skewed. However, a subsequent analysis by Gregory (1994) of the same but updated data base confirmed the left skew of the distribution but showed that this was not different from zero, implying that it could arise if we assume that the abundance of birds represents independent random draws from a log-normal distribution. A recent analysis by Gregory (2000) confirms the pattern of negatively skewed distributions in most European countries (40 out of 48, and significantly so in 10) and for both resident and migrant species, although this was less frequent in the latter (see also Gaston *et al.* 1997a). In Fig. 5.3a, we show the same pattern but for North American birds at the continental level, and at the level of states within North America (Fig. 5.3b–f). In all cases we used data from the Breeding Bird Survey (Peterjohn 1994). The distributions shown in Fig. 5.3 are significantly left skewed (one-tailed t-test $P < 0.05$), except for the states of Alaska and British Columbia.

The evidence discussed above suggests that the universe might not be as originally assumed by Preston (1948) or by Fisher *et al.* (1943), implying that there are many more rare species than previously believed, substantiating the claim that most species are rare. But how can we explain this pattern? Several explanations have been proposed in the literature, starting with Whittaker (1965) and the McNaughton & Wolff (1970) dominance model, and continuing with niche models (Tokeshi 1996, 1999), neutral models (Hubbell 1997; Bell 2000), self-similar models (Harte *et al.* 1999) and spatially explicit models (Chave *et al.* 2002). In what follows we will focus mostly on how niche models can bear on this pattern to show later how these models can be framed so as to be consistent with neutral models focused on birth–death processes in a spatially explicit framework.

Niche models

Niche models have a long tradition in ecological sciences, and several ecologists have devoted a large research effort, attracted by the beauty of their simplicity, whereas others have been discouraged by their restrictive assumptions.

The first model known to western scientists was MacArthur's (1957) broken-stick model, the immediate ancestor of which is found in Motomura's (1932) geometric series model (Fig. 5.1; see Whittaker 1965). Niche models simplify reality by considering that the environment, or niche space available for a group of species, can be represented by a stick of unit length, which can be broken following a particular rule. Once the stick is broken, subsequent species invading the local community must choose among the pieces available (following a choosing rule) and break it again. It is assumed that the length of the segment allocated to each species is proportional to its abundance within the community. Depending on the rule followed for choosing and breaking and on its nature (deterministic or stochastic), several models can be identified (for a review see Tokeshi 1993, 1997, 1999).

Whereas Motomura's model entails the fixed and sequential division of niche

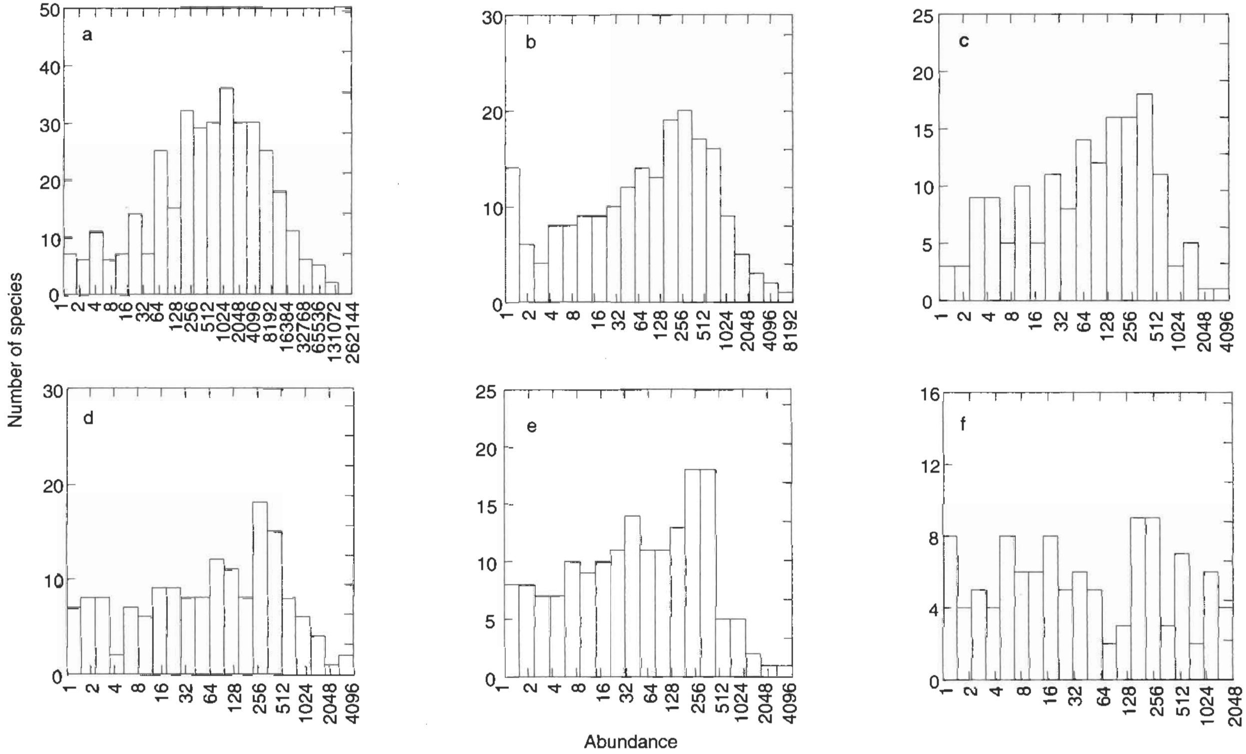

Figure 5.3 Distribution of abundance for 352 species of North American birds censused in June 2000 along 2366 routes of the Breeding Bird Survey (a) and State-level analysis of the distribution of abundance for 273 species of North American birds censused in June 2000 along 331 routes, in the States of California (b), Oregon (c), Washington (d), British Columbia (e) and Alaska (f).

space, such that each species invading the community takes a fraction *k* of the unused niche space, MacArthur's broken-stick model (MacArthur 1957) envisages a simultaneous process such that the stick of unit length is simultaneously partitioned at $n - 1$ points thrown at random. A similar model was later proposed by Sugihara (1980), however, this model was sequential and multidimensional, and purported to represent the breakage of several different niche axes. In testing his model, Sugihara (1980) showed that random selection of sticks and sequential breakages following a 0.75:0.25 proportionality instead of being random (Sugihara's fixed fraction model, SFF), fit the data better than MacArthur's model and also lead to a canonical log-normal distribution of abundances, which is not obtained if breakages are random in the interval (0,1). Sequential breakage, as originally envisaged by Motomura (1932), provides a more sensible analogy for how communities are built up, envisaging the successive carving out of niche space by species. A further addition to sequential niche models was introduced by Tokeshi (1990). This author recognizes six additional sequential models depending on how sticks are chosen and subsequently broken. Among them are the random fraction model (RF), where both processes are random, and the MacArthur fraction model (MF), which is the sequential version of the original broken-stick model. In this last model, the breakage is random but the stick selection probability is positively related to stick length. As shown by Tokeshi (1996), the RF and MF models are extremes of a more general model, the power fraction (PF) model, where the probability of stick selection is proportional to the sizes of existing niche fragments raised to the exponent *k*. A PF model with $k = 0$ corresponds to the RF model, whereas when $k = 1$ it corresponds to the MF model.

Niche models assume a zero-sum game, where the total number of individuals of all species together is essentially constant, such that increases in the population of some species result in corresponding decreases of others (MacArthur 1960). This means that most abundance distributions show a negative skew (Fig. 5.4), which is most apparent for the MF model, where rare species are more likely to accumulate because of the biased stick selection process it entails. In general, asymmetric segment division tends to exacerbate the negative skewness (Novotny & Drozd 2000).

Thus, negatively skewed distributions can be explained easily by niche models. As shown by Tokeshi (1996), the PF model with $k = 0.05$ gives rise to distributions that do not differ from that observed for British birds, and for *k* values in the range 0–0.2 the model fits data from a wide variety of species-rich assemblages. However, what is the precise biological meaning of the parameter *k*? Before attempting to answer this question we will examine the validity of one of the central assumptions of niche models. That is, that the apportionment of resources (stick fragments) is equivalent to the apportionment of individuals (abundance).

How do species divide resources?

Sugihara (1980) clearly established the main assumption of niche apportionment models (p. 773) '. . . because a niche translates ultimately into number of organisms (or biomass), observed abundance patterns can offer a useful standard measure of

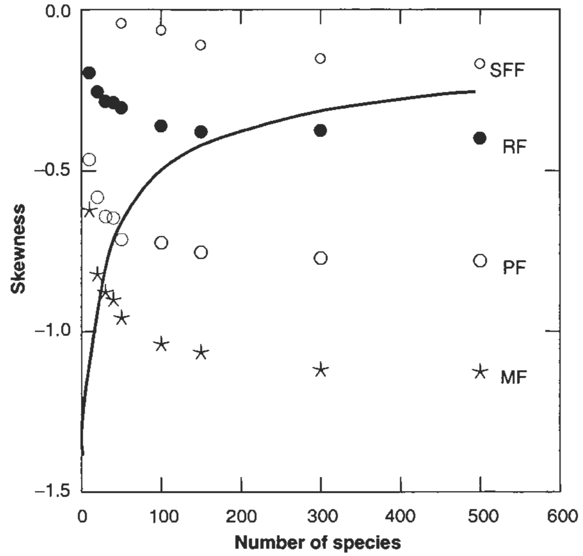

Figure 5.4 Changes in average skewness with number of species. Each value corresponds to the average calculated over 500 simulations for the random fraction (RF), MacArthur's fraction (MF), Sugihara's fixed fraction (SFF) and power fraction (PF, $k = 0.5$) models. The solid line shows the critical value ($\alpha = 0.05$) of skewness.

niches . . .' As is clear from this statement, niche models assume that the abundance of a species is a reflection of the amount of limiting resources it controls, such that knowledge of how resources are divided among species within communities would allow us to predict abundance patterns. The first test of this assumption was attempted by Harvey & Godfray (1987). These authors point out that Sugihara's model assumes that the way individuals and resources are apportioned to communities are equivalent processes, which would work if individuals of all species are equivalent. However, most species are likely to differ in body mass, which scales with both population density and per capita resource requirements such that both processes might not be equivalent. They notice that if population density scales with body mass (e.g. Damuth 1981, Peters 1983) as

$$N \propto M^{-x} \tag{5.1}$$

and that according to Kleiber's law per individual energy requirements (P) increase with body mass as

$$P \propto M^{y} \tag{5.2}$$

then substituting equation (5.1) into equation (5.2), and considering that according to (5.1) $M \propto N^{-\frac{1}{x}}$ per individual energy requirement can be expressed as

$$P \propto \left(N^{-\frac{1}{x}}\right)^{y} \propto N^{-\frac{y}{x}} \tag{5.3}$$

Then, the amount of energy used per unit area by a population ($E \propto P \times N$) would be equal to $E = c \times N^{\left(1-\frac{y}{x}\right)}$, where c is a normalization constant. Therefore

$$\log(E) = \log(c) + \left(1 - \frac{y}{x}\right)\log(N) \tag{5.4}$$

If $\log(N)$ is normally distributed across species, then $\log(E)$ also will be, and its variance will be

$$V(\log E) = \left(1 - \frac{y}{x}\right)^{2} V(\log N) \tag{5.5}$$

From equation (5.5) it is apparent that if $x \approx y$ then $V(\log E)$ will tend to zero, and the expected value of $\log(E)$ will be constant and independent of population density (as has been reported under the Energetic Equivalence rule; Damuth 1987; Nee *et al.* 1991b; Marquet *et al.* 1995; Enquist *et al.* 1998). Further, as x is less than $2y$ in most studies, then $V(\log E)$ will be lower (more equitable) than $V(\log N)$. Hence, from this perspective the apportionment of individuals and resources might not be equivalent processes, which is the main assumption of niche models. However, as pointed out by Sugihara (1989) these authors assume that the allometric equations they used had no error variance (no scatter), implying that this has no impact upon the total variance estimate for biomass and E. Interestingly, once error variance is considered, error propagation also becomes a problem. As demonstrated by Taper & Marquet (1996) the estimates of $V(\log E)$ derived by Harvey & Godfray (1987), Sugihara (1989) and later by Pagel *et al.* (1991) were all derived under the implicit assumption that population density influences body size, which in turn influences metabolic rate and consequently population energy use. Taper & Marquet (1996) show that if we solve for M in equation (5.2) and substitute it to equation (5.1) we arrive at an alternative expression for $V(\log E)$, but this time assuming that P causes or determines M, which in turn determines or causes N. These authors identify three potential models, with different expressions for $V(\log E)$, and specify different pathways of error propagation, which they label N causal, P causal and M causal models.

Although there is no objective way of deciding which model best describes reality, traditionally body size has been assigned a causal role in the study of a variety of physiological, ecological and evolutionary phenomena (e.g. Peters 1983; Calder 1984; Brown & Maurer 1986; Brown *et al.* 1993), thus it seems biologically reasonable to use the M causal model to assess if the apportionment of individuals and resources are equivalent processes.

Under this model $V(\log E)$ is expressed as

$$V(\log E) = \left(1 + \frac{y}{x}\right)^{2} [V(\log N) - V(d_n)] + V(d_n) - V(d_p) \tag{5.6}$$

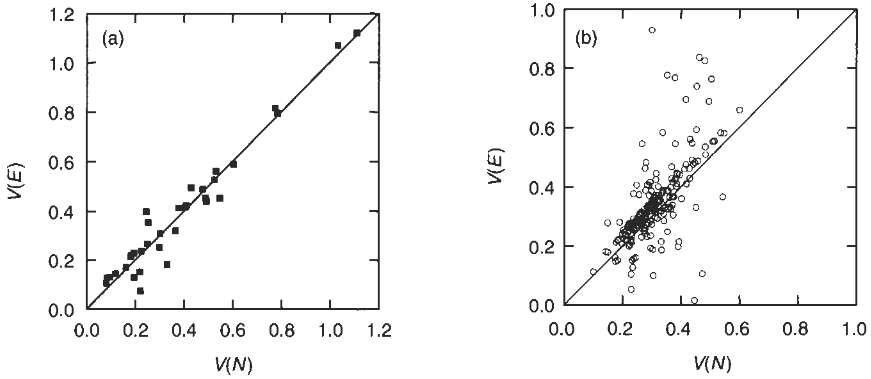

Figure 5.5 Relationship between the variance in population energy use $V(E)$ and variance in population density $V(N)$. (a) Relationship calculated for 41 bird communities reported by Brown & Maurer (1986) and recalculated from Taper & Marquet (1996) using $V(d_p) = 0.03$. (b) Relationship calculated for 204 Breeding Bird Survey routes that satisfied the criteria of having more than 20 species with a relationship between body size and abundance of $R^2 > 0.1$.

where $V(d_n)$ and $V(d_p)$ are the error variances associated with equations (5.1) and (5.2) respectively. The analysis of 41 local bird communities compiled by Brown & Maurer (1986) shows an almost perfect agreement between $V(\log E)$, estimated by equation (5.6), and $V(\log N)$ (see Fig. 5.5a). Further, an expanded analysis using the data compiled by the Breeding Bird Survey for those routes in the states of California, Oregon, Washington, Alaska and British Columbia (Fig. 5.5b) shows that there is a good correlation between both variables ($r = 0.66$, $P < 0.001$, $n = 204$), despite the fact that these data are considerably less accurate than those compiled by Brown & Maurer (1986). Thus, based on this evidence we can conclude that the apportionment of individuals and resources are equivalent processes, which validates the central assumption of niche models. However, their usefulness ultimately will depend on the biological plausibility of the sequential apportionment process they entail. This returns to the question of the meaning of k.

On the meaning of *k*

According to Tokeshi (1996), k has an ecological and evolutionary meaning. In ecological terms it implies that communities are built up by a sequential niche apportionment process, whereby the probability of niche division or invasion of existing niche space is slightly higher for species with larger niches or higher abundance. Evolutionarily, k is related to the probability of speciation, such that $k > 0$ means that species with higher abundance, which also tend to have larger geographical ranges (see review by Gaston *et al.* 1997b; Gaston & Blackburn 2000), are more likely to generate new species. Interestingly, the distribution of range sizes is also left-skewed after logarithmic transformation, which suggests a potential connection between both patterns (Gaston 1998; Gaston & Blackburn 2000; Gaston & He 2002). However, although this argument is plausible, because larger ranges are more likely to be intercepted by barriers, the evidence at best is equivocal and depends critically on assumptions about the distribution and type of barrier sizes (Gaston 1998).

In any case, is not obvious that the PF model can account for the positive correlation between distribution and abundance. To see this, assume that we have a large number of communities in a large geographical area, and that each species that invades a community will reach a local abundance as dictated by the PF model. In this scenario, for a positive relationship between range size and abundance to arise would require an almost perfect spatial synchronization in the sequence of invasion, such that each species invades all local communities at about the same time, and the existence of a lower threshold of abundance such that smaller sticks are associated with higher probability of local extinction. Clearly, such a process would entail the use of spatial models incorporating the dynamic processes of invasion and extinction. In this regard, metapopulation models (e.g. Levins 1969; Hanski 1999) represent a natural point of departure.

Breaking the stick in space

Niche models emerged as a statistical approach to understand patterns of abundance in samples of local communities. The original emphasis was on proposing mechanisms of resource division that might account for the observed patterns. However, since their inception in ecology, much emphasis has been put on testing how adequately the models fit reality (e.g. Tokeshi 1990; Naeem & Hawkins 1994; Bersier & Sugihara 1997) and less on trying to understand the biological meaning of their parameters and underlying assumptions. In particular, the PF model proposed by Tokeshi (1996) is flexible enough to be able to fit most of the observed patterns in abundance by varying the parameter *k*, the meaning of which, as already discussed, is not yet clear. However, in addition to this constraint on explanatory power and biological relevance, available evidence indicates that the basic assumption of equivalence between the processes of apportionment of individuals and resources holds. As we will show below, this fact permits a link between resource acquisition, resource conversion and space occupation processes. As for niche models, there is still much room for improvement. Among other things, niche models are static, the number of species is not a result of the model, but a free parameter specified by the investigator, and because they are not spatial it does not matter how species arrive and persist in local communities, hence they do not incorporate any mechanistic link with the basic processes of fecundity and mortality (Hubbell 2001). Interestingly, metapopulation models of the patch-occupancy type (Levins 1969) have some key ingredients that might serve the purpose of making niche models dynamic and linked to species life-history attributes. On the other hand, multispecies metapopulation models (i.e. metacommunity models) might take advantage of the simplicity of the niche apportionment process to generate within-patch dynamics in abundance.

Metapopulation models, of the patch-occupancy type, assume that the environment is composed of a large number of identical patches that either can be empty or occupied by a local population. In these models, the proportion of patches (p) that a species occupies in a given area is driven by the rates of colonization (f) and local extinction (e)

$$\frac{\mathrm{d}p}{\mathrm{d}t} = fp(1-p) - ep \tag{5.7}$$

At equilibrium, the proportion of occupied patches is given by $\hat{p} = 1 - \frac{e}{f}$, thus, a positive proportion of occupied patches at equilibrium will exist whenever $\frac{f}{e} > 1$. Taking into account that the average lifetime of an occupied patch is $\frac{1}{e}$, the above expression represents the total number of secondary colonizations produced by an occupied patch during its lifetime. This threshold parameter corresponds to the basic reproductive number used in epidemiology (usually denoted by the symbol R_0), where it measures the number of secondary infections that a single infectious individual produces when introduced in a completely susceptible population (Diekman *et al.* 1990; Hernández-Suárez *et al.* 1999). If this number is greater than 1, the disease spreads in the host population. The basic reproductive number is therefore an invasion criterion: it determines if a pathogen will be able to survive in a host population once it is introduced. In a metapopulation context, it determines if a landscape composed of a set of empty patches will be colonized successfully, and also determines its long-term persistence (Marquet & Velasco-Hernández 1997). To appreciate the importance of R_0 in affecting metapopulation persistence, we can rescale time in equation (5.7) by taking as a unit the average time to extinction $\frac{1}{e}$. With this rescaling, Levin's original model becomes

$$\frac{\mathrm{d}p}{\mathrm{d}\tau} = R_0 p(1-p) - p \tag{5.8}$$

where τ stands for the new rescaled time (Hernández-Suárez *et al.* 1999). It is clear in equation (5.8) that if $R_0 < 1, p \to 0$ and if $R_0 > 1, p \to 1$.

In this model, if the site can accommodate only one individual, p becomes the regional abundance of a species (Tilman 1994), the colonization rate f becomes the rate of propagule production by one individual or fecundity, and the extinction rate becomes an individual mortality rate (m). As before, the equilibrium abundance for a species with a given f and m becomes $\hat{p} = 1 - \frac{m}{f}$. Multispecies versions of this model incorporating competitive interactions among species, as well as their spatial analogues, have been widely analysed in the literature (e.g. Hastings 1980; Tilman 1994; Kinzig *et al.* 1999). As a point of departure let us analyse the simplest multispecies model, one where species compete for space, such that once an individual of species i arrives at a site it makes it unavailable for others until it dies.

This model can be written as

$$\frac{\mathrm{d}p_i}{\mathrm{d}t} = f_i p_i \left(1 - \sum_{j \neq i} p_j - p_i\right) - m_i p_i \tag{5.9}$$

The first term on the right-hand side gives the colonization of empty habitat patches (i.e. individuals) and the last term the extinction of habitat patches. This mean-field equation can be converted easily to a spatially explicit model, which we will call the basic contact process with no-sticks. First, however, it should be noticed that in this model the equilibrium abundance of species will depend on their $R_0 = \frac{f}{m}$, but weighted by the availability of resources (empty space); we will call this weighted R_0 the realized R_0. To see this we can rescale equation (5.9) (see Kinzig *et al.* 1999; Dushoff *et al.*, in press) by defining the quantity $\theta = 1 - \sum_{j \neq i} \hat{p}_j$ as the number of sites not occupied by species other than i after each species j has reached its equilibrium abundance ($\hat{p}_j$).

Using this quantity the equilibrium abundance of species i can be expressed as

$$\hat{p}_i = \left(\frac{\theta R_0 - 1}{R_0}\right)$$

Unlike equation (5.7), now the equilibrium abundance is a function of the species life-history and the abundance of resources in the environment, such that persistence will be possible only if the condition $\theta > \frac{1}{R_0}$ is satisfied. This relationship between life-history attributes, resource availability and persistence is essential to forge a link between the resource apportionment process and birth–death processes.

To construct a spatial version of this model let us assume a regular homogeneous lattice of 256 × 256 sites in a torus such that each lattice site has the same number of neighbours. Each site can accommodate one individual, and can be either occupied or empty, such that the number of occupied sites translates to regional abundance (N). The model dynamics are given by the species fecundity (f) and mortality (m) rates. Fecundity rate is the expected number of birth events by an individual during a unit time interval. Newborns are sent to nearest-neighbour sites with equal probability, but establish only if the landing site is empty. Similarly, each individual dies at a constant rate (i.e. the expected number of death events in a unit time interval). Thus species follow a contact process type of dynamics (Durret & Levin 1994a,b). The model is initialized by randomly seeding the landscape with n species, each in 0.1% of the sites; no further seeding is allowed.

As is well-known for these models (Neuhauser 1992), in the long-term, the species with the largest R_0 will reach the highest abundance, and eventually displace all others, achieving complete occupancy if its reproductive number is greater than 1. However, the transient dynamics towards this equilibrium can be very long and give rise to left-skewed distributions of abundance (Fig. 5.6). Thus, under non-equilibrium conditions this model predicts distributions of abundance qualita-

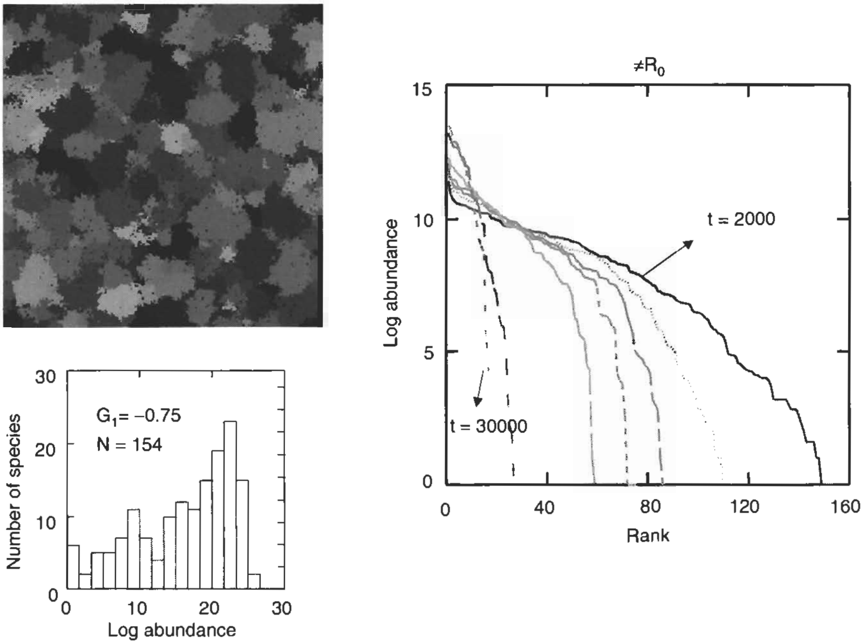

Figure 5.6 Transient dynamics in the spatially explicit pre-emptive competition model run in a lattice of 256 × 256 sites. The model was started with 10 000 species randomly seeded in 1% of sites. Each species was randomly assigned a fecundity and mortality value drawn from a uniform distribution between 0 and 1. The resulting transient spatial pattern is shown on the upper left panel for $t = 2000$, where different intensities of grey correspond to different species, and empty cells, owing to the death of an individual, are shown in black. The panel in the upper right shows the rank–abundance plots for different time-steps. The lower left panel shows the distribution of abundance for 154 species for the time-step = 2000. Notice that the distribution is strongly left-skewed, as was also observed for all other time-steps.

tively compatible with empirical data as a result of all but one species going randomly extinct in time. A similar pattern emerges when all species have equal R_0 (Fig. 5.7; $f = 0.7$, $m = 0.2$), with the important distinction that in this case any species can win and the dynamics is a random walk towards either extinction or occupation of all available space, which is proportional (but not exactly equivalent, because of spatial correlations) to $\hat{p} = 1 - \frac{m}{f}$. Under these conditions species follow a zero-sum ecological drift (Hubbell 2001).

This model is suitable for understanding the dynamics of species undergoing competition for space in a closed community (i.e. without immigration from outside the system). Our next step will be to build a metacommunity model of species competing for food resources, as assumed in traditional niche models. Our aim here

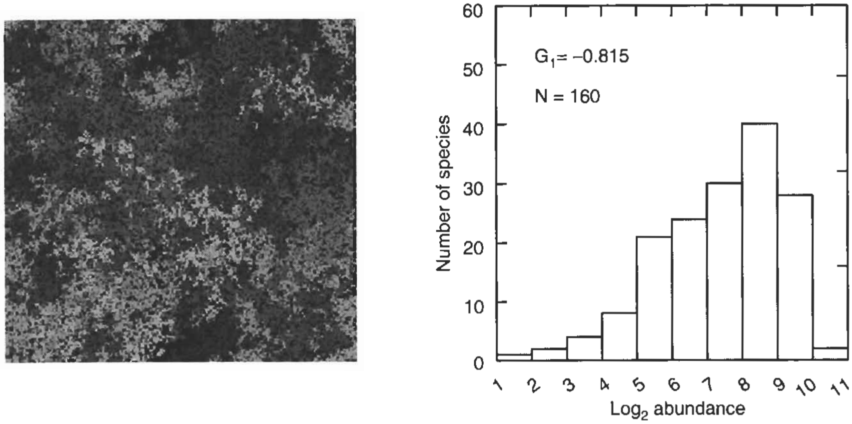

Figure 5.7 Same as in Fig. 5.6 but this time under conditions of ecological equivalence where each species had the same fecundity ($f = 0.7$) and mortality ($m = 0.2$). The results shown correspond to the time-step = 3500.

is to link niche models with those based on birth–death processes (e.g. Hubbell 2001).

Our model (Keymer & Marquet, unpubl.) links together the acquisition of energetic resources (E_1) with the appropriation of space through a simple transformation inspired in a model originally developed by Brown *et al.* (1993), which envisages organisms as operating a transformation on the environment

$$E_1 + I_0 \rightarrow I_1 \tag{5.10}$$

$$I_1 \rightarrow I_0 + b \tag{5.11}$$

$$b + S \rightarrow I'_0 \tag{5.12}$$

Under this model, an organism without resources for reproduction (I_0) acquires them from the environment, forming an unstable individual–resources complex (I_1) (equation 5.10) and decaying back to an individual without resources but using the captured energy to make a potential copy of itself (b) (equation 5.11) at a rate f which will later react with a position in space (S) to become a full self-reproducing copy (I'_0).

This framework allows us to couple resource acquisition processes (niche breakage) with space occupation. Assuming equal mortality and longevity and no resource limitation, the intrinsic reproductive number of species i becomes $R_{0,i} = f_i$. However, if resources are in fact limiting (i.e. the length of the stick is finite as assumed in niche models) the reproductive number of species i will be given by the amount of resources it can capture (stick length, x_i). In turn for each species i we can define a realized reproductive number $R_{0,i}$ that will be a function of the stick length

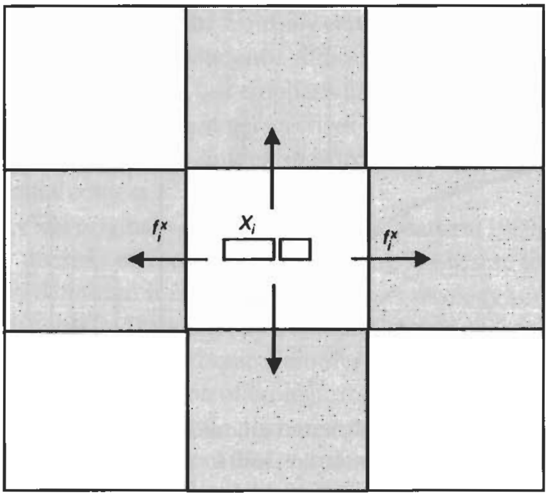

Figure 5.8 Schematic representation of the lattice model.

$$R_{0,i}(x_i) = R_i \times x_i \tag{5.13}$$

Keymer & Marquet (unpubl.) describe in detail the spatial model resulting from letting this process unfold in space. Here we will provide a summary description.

Consider a two-dimensional regular lattice, wherein each cell represents a local community holding a stick of unit length to be apportioned among invading species (Fig. 5.8). Once a species arrives it will break the stick (according to Tokeshi's (1996) PF model with parameter k), appropriating a fraction x_i of available resources and producing propagules according to equation (5.13). Each propagule will disperse randomly to one of its four local neighbours (contact process-like) and invade the community located therein. At each local community populations can become extinct at a constant rate μ, and the released stick is proportionally reassigned among the locally extant populations. Under the assumption of ecological equivalency (equal $R_{0,i}$) and $\mu > 0$ the system has a long transient and eventually one species reaches total dominance for any k. In the transient phase, distributions of abundance are left-skewed (Fig. 5.9) as would be expected if species randomly walk to extinction. However, when $\mu = 0$ and $k = 0$ (RF model), species do not go extinct but maintain a statistical steady state and give rise to symmetrical log-normal distributions of abundance (Fig. 5.10a). A similar situation occurs for $k = 1$ (MF model), but this time the distribution is left-skewed (Fig. 5.10b) as a consequence of a biased stick-breakage process.

Spatial niche apportionment processes can generate a wide spectrum of distributions of abundance, some of which are in agreement with the patterns observed for the non-spatial models. This especially is evident when there is no local extinction of populations and under the assumption of ecological equivalency. When $\mu > 0$, the

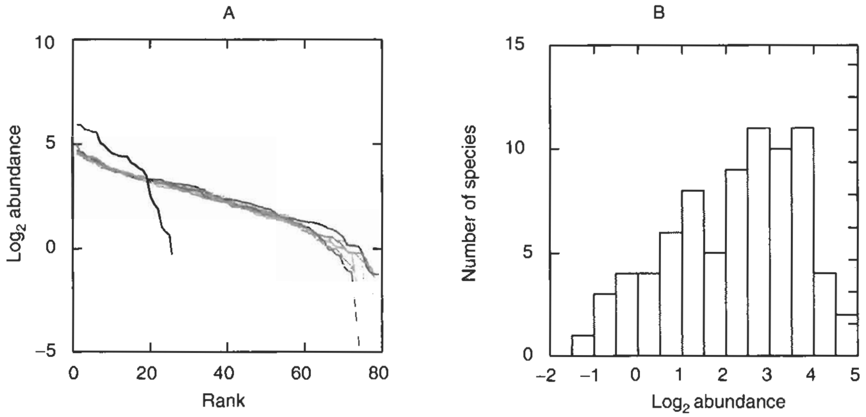

Figure 5.9 Results of the spatially explicit stochastic niche model for 100 species in a system of 1024 local communities (i.e. 32 × 32 lattice) with $k = 1$, which corresponds to the MacArthur fraction niche apportionment model. Local extinction probability was $\mu = 0.01$, and fecundity $f_i = 1$. The rank–abundance plot (A) is shown for the model at different time-steps (10, 20, 40, 60, 80, 100 and 160). The number of species present in the system decreases in time owing to extinction. The frequency distribution of abundance (B), as shown for $t = 60$, was left-skewed for all time-steps.

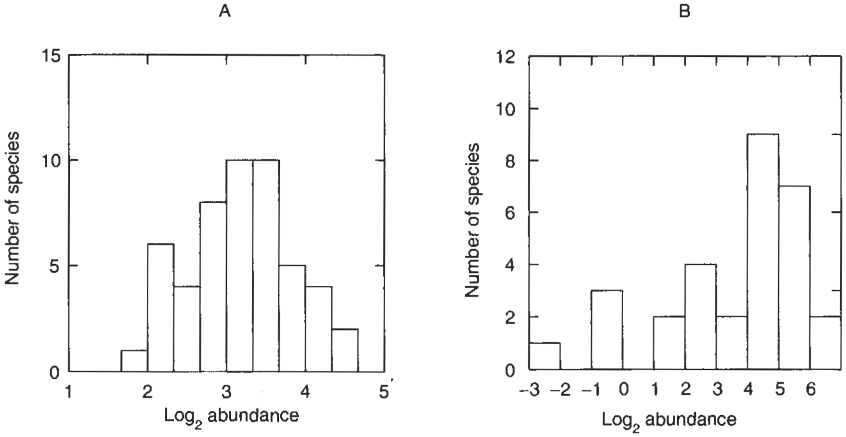

Figure 5.10 The same as in Fig. 5.9, but for 50 species with $\mu = 0$, and (A) $k = 0$ and (B) $k = 1$.

dynamics do not reach an attractor and one species eventually wins. Local extinction allows the liberation of resources and their capitalization by those species that already hold large sticks, a process that in the long term leads to a random walk to extinction for most species and the dominance of one. These simple spatially explicit stochastic models allow us to put traditional niche models in a dynamic context, linking resource acquisition with the fundamental processes of birth and death, thus showing that niche models can be fruitfully expanded to account for community patterns in the distribution of abundance. Although the patterns that emerge qualitatively resemble empirical data, our emphasis has been on providing a framework for reconciling these two divergent perspectives on the emergence of patterns. We showed that this is possible by linking resource and individual apportionment processes in a spatial context.

Macroecology was originally defined by Brown & Maurer (1989) as the search for patterns in the division of food and space among species at continental scales. Although in this definition it is debatable that macroecology is restricted only to the analysis of patterns and processes operating at the level of continents, the way in which organisms divide food and space resources seems to be fundamental to our understanding of the organization of ecological systems at any scale, and provides the basis for connecting local-scale phenomena, linked to niche apportionment processes, with patterns emerging at the level of metacommunities.

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