DYNAMICS OF DISTRIBUTION IN ANIMAL COMMUNITIES: THEORY AND ANALYSIS

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SUMMARY

Theoretical and analytical problems of the dynamics of distribution and abundance in animal communities were examined. In many communities, species with low abundance and of limited spatial occurrence (i.e., rare species) typically form a conspicuous peak when a frequency distribution of the number of species is constructed with respect to the proportion of sites occupied within an area of distribution. Models of distribution dynamics, including a new model proposed here, were compared with a range of animal community data using a new procedure to assess single- and bi-modal patterns in frequency distributions of spatial occurrence. Data reveal that single-modality with an excess of rare species occurs more frequently than bimodality. Even when bimodality is detected, the mode representing wide-spread species is in the majority of cases smaller than that for rare species. Thus, a new model in which the rate of local extinctions is assumed to be negatively related to patch occupancy (or population abundance) is in better agreement with observed data than earlier models. Some problems of analysis, in particular model assumptions and testing, are discussed.

KEYWORDS: distribution dynamics, extinction rate, modality patterns, distribution-species frequency data, animal communities.

INTRODUCTION

Distribution and abundance are two inter-related aspects which together constitute a central issue in modern ecological thinking (Andrewartha and Birch, 1954; Krebs, 1985; Begon et al., 1986). In theory the total abundance of a species is the sum of abundances of patchily-distributed populations (c.f., the metapopulation concept, Levins, 1971; Wilson, 1975; Slatkin and Wade, 1978) which encompass underlying spatial variation in the rates of population increase (i.e., reproduction and immigration) and decrease (death and emmigration). Thus *distribution*, the spatial extent of a species, is intricately related to the spatial variation in *abundance* (numerical extent) of local populations. Technically distribution and abundance can be

considered separately, with the latter having been subjected to more extensive theoretical analyses than the former (e.g., Anderson et al., 1979; May, 1975, 1981). In parallel to this it has been recognized that spatial variation or heterogeneity, a ubiquitous trait of organismal distribution, is an important component in the dynamics of species' abundances (e.g., Roughgarden, 1974; Lomnicki, 1980; Kareiva, 1987). Similarly, even in a largely static, descriptive approach of so-called 'species abundance patterns', it is possible to incorporate stochastic variability (which may relate to spatial as well as temporal aspects) in the models (c.f., Engen, 1978; Tokeshi, 1990a, 1992). It has also been suggested that a better understanding of ecological communities may emerge from an integrated approach to distribution and abundance (Hanski, 1982a). A number of works examined the patterns of spatial distribution and abundance in various communities (e.g., Hengeveld and Haeck, 1981, 1982; Hanski, 1982a, b, c; Brown, 1984; Gaston and Lawton, 1990; Collins and Glenn, 1990; Gotelli and Simberloff, 1987). Despite this background, the issue on the whole is still unresolved while other relevant theoretical aspects seem to be left largely unexplored (c.f., Maurer, 1990).

In the context of the distribution/abundance problem, one of the most abiding and conspicuous phenomena of ecological communities is the existence of a large number of species with very low abundances. It is intuitively clear that species with low abundances are on average more likely to be associated with reduced spatial occupancy than those with high abundances. Thus a community tends to consist of many species forming a spatial 'mosaic' whilst a small number of species occur ubiquitously over the community range. Despite the universality of this pattern, there has been very few attempts to elucidate its possible theoretical basis and dynamic characteristics. One interesting development in this direction is Hanski's (1982a) model of spatial dynamics which is a modification of Levins' (1969, 1970) model relating to local extinction and immigration of species. These models are structurally simple but represent an important step towards unravelling the metapopulation dynamics. In particular, Hanski (1982a) suggested that a stochastic version of his model predicts a bimodal frequency distribution of species occupying patchily-distributed sites within the region of their occurrence, such that species are classified either as core species (occuring in almost all the sites) or as satellite species (occuring in a few sites). It is notable here that his model did not lead to unimodality of rare species (which ecologists might expect to be a general case) but bi-modality with almost equal abundances of wide-spread species as rare ones (see section on THEORY). A number of workers who tested this hypothesis with various animal and plant taxa generally took the view that the data were in agreement with the hypothesis (e.g., Hanski, 1982a, b, c; Gotelli and Simberloff, 1987; Collins and Glenn, 1990, 1991), while Gaston and Lawton (1989) argued that neither Bracken insects nor most other animal assemblages supported it. The comparableness and implications of these results with respect to the core-satellite hypothesis may be called into question because

of different methodologies and criteria used for testing one vital point in this issue—modality. In a broader context, specific conditions which lead to Hanski's (1982a) model need to be understood more clearly before an attempt is made to infer its implications for a particular community (e.g., Gaston and Lawton, 1989). One of the key assumptions of Hanski's (1982a) model, positive correlation between local abundance (generally expressed as log average abundance) and regional distribution—note here that Gotelli and Simberloff (1987) and Gotelli (1991) interpreted this as a *prediction* of the model, while Gaston and Lawton (1989), Nee et al. (1991) and Hanski (1991b) himself clearly treated this as an *assumption*—, is widely observed in real communities (e.g., Hanski, 1982a; Bock and Ricklefs, 1983; Brown, 1984; Bock, 1987; but see Gaston and Lawton (1990) for cases where abundance is expressed as local abundance in a particular 'reference habitat'). However, another key assumption relating to frequent switching of species from core to satellite status and vice versa does not seem to have been confirmed, thus casting doubt on the applicability of this model to natural communities. At the same time, there is one important characteristic in Hanski's original model that has not previously been recognised explicitly in testing the model, i.e., the mode for the core species would be larger than that for rare species (see THEORY). The issue of testing the core-satellite hypothesis with real communities is further compounded by Hanski's (1991a) alternative model which is claimed to predict bimodality in distribution without the need for core-satellite switching. Thus, the vagueness of models themselves and problems of modality testing combine to make this a rather confusing area, despite the potential importance of the concept of metapopulation dynamics in basic population/community ecology and its applied fields such as conservation ecology and agricultural pest management (c.f., Hanski and Gilpin, 1991).

The objective of the present paper is three-fold. First, characteristics of models by Levins (1969, 1970) and Hanski (1982a) are re-examined, with some emphasis on clarifying the original core-satellite hypothesis. In conjunction with this, a new model is proposed which closely relates to earlier models by Levins and Hanski. Particular attention is drawn to the differences in modality patterns predicted by these models. Hanski's (1991a) alternative model, which is developed on somewhat different frameworks compared with earlier models, is also considered but analysis is limited due to uncertainties of proposed parameters. Consideration is also given to Gotelli's (1991) modification of Levin's and Hanski's models. Second, in consideration of the difficulties associated with testing different hypotheses, a new procedure is introduced as a standard criterion for detecting modality trends which is universally applicable to distribution—species frequency data. Third, data on a wide range of animal communities, including a freshwater chironomid community that has not previously been examined in this context (Tokeshi, 1986a, b, 1990a, b; Tokeshi and Townsend, 1987), are subjected to an analysis with the exact probability method to see their conformity with different model predictions. An overall picture to emerge from this

analysis is that the new model gives a better explanation of the rare-majority paradigm (i.e., an abundance of rare species in a community), which is widely observed among natural communities.

<p style="text-align:center">THEORY</p>

Two-Parameter Models

Theory of the dynamics of distribution closely parallels the theory of island biogeography developed by MacArthur and Wilson (1967). In essence, models of distribution dynamics describe the change in the proportion of habitat units occupied, p, in terms of the difference between the rates of colonization (immigration) I and of extinction E,

$$dp/dt = I - E .$$

Consequently, different assumptions concerning I and E lead to different patterns. The first model was proposed by Levins (1969, 1970),

$$dp/dt = ip(1-p) - ep \qquad (1)$$

where i and e (both >0) are parameters relating to colonization and extinction, respectively. The first term in this equation, $ip(1-p)$, representing the rate of colonization, is based on the assumption that the colonization rate is related to the abundance of colonising individuals (roughly corresponding to p) and to the proportion of unoccupied sites $(1-p)$. The second term, ep, describes the rate of local extinctions as a linear function of p. Subsequently, Hanski (1982) suggested a modification to this model to enhance reality,

$$dp/dt = ip(1-p) - ep(1-p) . \qquad (2)$$

Note that the difference between the two models concerns the second term only, where the inclusion of $(1-p)$ in Eq. (2) implies a decreasing probability of local extinction with large population size, or 'rescue effect' (MacArthur and Wilson, 1967; Brown and Kodric-Brown, 1977).

Yet another possibility is that, while accepting the importance of rescue effect (i.e., inclusion of $(1-p)$ in the second term), the overall extinction rate is assumed not to be a direct function of the current level of habitat occupancy (p); thus, eliminating p from the second term of Eq. (2),

$$dp/dt = ip(1-p) - e(1-p) . \qquad (3)$$

These three models (hereafter called model 1, 2 and 3, respectively) agree in that the change in p is described as a difference between the rates of colonization and extinction. Furthermore, all of them assume that the rate of colonization is proportional to the abundance of potential colonizers (represented by p, which roughly

reflects abundance) as well as to the proportion of empty sites available for colonization $(1-p)$. Attention therefore needs to be drawn to the description of the rate of local extinctions where the difference lies between the models.

In model 1 (Eq. (1)) the rate of extinction is a linearly increasing function of p, assuming a minimum value $(=0)$ at $p=0$ and a maximum $(=e)$ at $p=1$, while in model 2 (Eq. (2)) it is a parabolic function of p with a maximum value $(=e/4)$ at $p=0.5$, gradually declining to a minimum $(=0)$ as p is displaced towards either of the two boundary values (i.e., $p=0$ or 1.0). In contrast, model 3 describes the rate of extinction as a linearly decreasing function of p, with a maximum $(=e)$ being achieved at $p=0$ and a minimum $(=0)$ at $p=1$. Notwithstanding the gross simplifications involved here, the appropriateness of different assumptions concerning the description of the rate of extinction can roughly be assessed by examining real data. Fig. 1 illustrates the relationship between the rate of local extinction, calculated as the mean proportion of island habitats occupied in year 1 which became unoccupied in year 2, and habitat occupancy (proportion of islands occupied, p) in year 1, based on the data of arthropod communities on mangrove islands (Simberloff, 1976). This shows that the rate of extinction (corresponding to the second term of Eq. (1)–(3), which should not be mixed with what Hanski (1982a) referred to as the probability of extinction) neither increases with p (model 1) nor has a parabolic relation (model 2) but declines

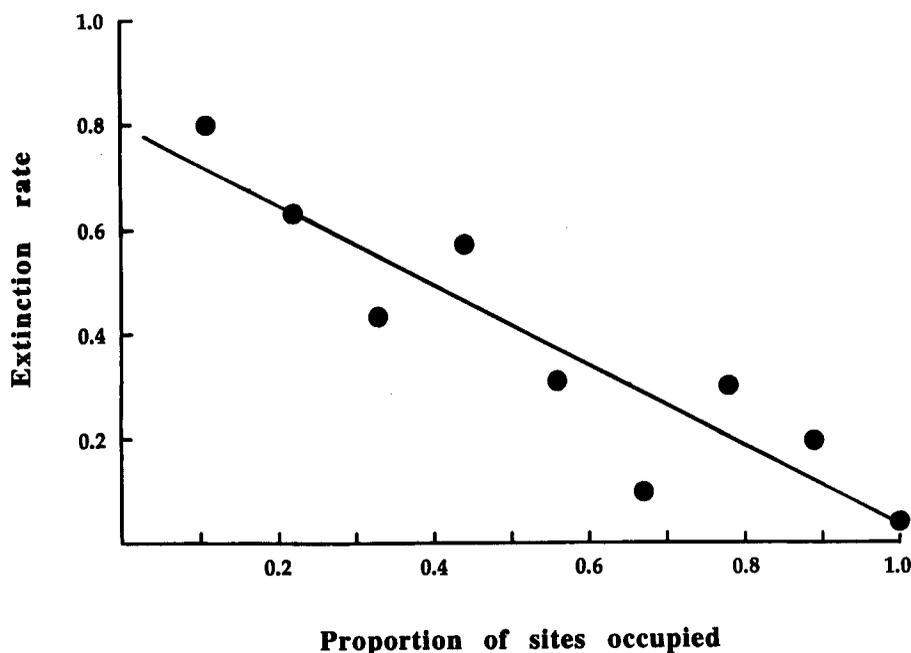**Proportion of sites occupied**

Fig. 1. Relationship between the rate of extinction and the proportional occupancy of habitats among 205 species of arthropod on mangrove islands (data from Simberloff, 1976). The rate of extinction is an average value for all the species occupying the same number of islands in year 1. $y=0.797-0.761x$, $r=0.914$, $P<0.001$.

with increasing p as described by a simple linear approximation of model 3. Thus there is no concrete reason at this stage to disfavour model 3 in comparison with earlier models 1 and 2, in terms of describing the rate of extinction.

Assumptions and Predictions

The relative magnitudes of i and e are very important in determining the outcome of models 1 to 3. Thus any assumption relating to i and e, such as a large stochastic variation in $(i-e)$ postulated by Hanski (1982a) for his model, needs to be carefully examined with reference to all these models. If colonization parameter i is consistently smaller than extinction parameter e, all the models predict that a species will become rare or extinct. Therefore it is perhaps trivial to assume a uniform occurrence of $i<e$ across species in a community; such a community is doomed to disappearance and serves as a poor comparison to extant communities under investigation. However, this does not necessarily exclude the possibility of i becoming smaller than e with certain frequency; all what is reasonably required here is that, on average, i is larger than e. This point is in fact crucially important in establishing Hanski's core-satellite hypothesis (1982a).

Assuming that $i \geq e$ holds on average whilst allowing for (at least) some level of stochastic variation in these parameters, it is useful to classify two cases: (i) i and e are stochastically variable but always satisfies $i \geq e$; (ii) i and e are stochastically variable and sometimes $i<e$, but on average $i \geq e$ holds true. Under the case (i), model 1 leads to a single, stable equilibrium point in p $(=1-e/i)$. Thus a community of species all behaving in this way but independently of each other (see section 'Problems of extrapolating from single-species to multi-species patterns') will produce a uniform frequency distribution of species in terms of the extent of spatial occurrence, or the proportion of sites occupied p (Fig. 2). In contrast, with $i>e$ always holding in model 2, a species will invariably achieve cosmopolitan occurrence $(p \rightarrow 1.0)$, so an assemblage of species will produce a single mode at $p \approx 1$ in a frequency distribution (Fig. 2, model 2, left). The patterns expected from model 3 will be more complicated, because the final outcome depends on the value of p in relation to e/i ; a species will either be rare $(p \approx 0)$ or wide-spread $(p \approx 1)$. When this is extended to a large number of species in a community, the resultant pattern of frequency distribution will be bi-modal at $p \approx 0$ and 1 (Fig. 2, model 3, left).

The assumption of the case (i) described above may be rejected on the ground that the natural world always encompasses a substantial amount of stochastic variation (environmental, demographic and other population/community traits) and the rate of colonization/extinction is no exception (c.f., Hanski 1991a); it is inevitable that e is larger than i on some occasions. Then the case (ii) can be applied to the models, leading to qualitatively different predictions. With $\bar{r}$ and σ_r^2 denoting, respectively, the mean and variance of $r=i-e$, Hanski (1982b, c) postulated,

$$\sigma_r^2 > \bar{r} > 0 \tag{4}$$

which corresponds to the case (ii). However, it should be stressed here that this condition (4) does not automatically induce a bimodal frequency distribution from Eq. 2. As Hanski (1982c) himself stated, stochasticity needs to be substantial, i.e., σ_r^2 being ten times or more greater than $\bar{r}$, to produce bimodality; if not, single modality with a mode at $p \approx 1$ will result. Thus the rates of colonization and extinction within a species are suppose to fluctuate wildly in Hanski's model. It should be noted at the same time that, with the condition embodied in Eq. (4), the mode at $p \approx 1$ is always expected to be larger than that at $p \approx 0$. This is an inevitable outcome of Hanski's assumptions, which is clearly demonstrated in the results of his own simulations (see Fig. 2 of Hanski, 1982c). However, this has been largely overlooked in the later works testing Hanski's model (e.g., Gotelli and Simberloff, 1987; Collins and Glenn, 1990).

Under the case (ii) in model 1, a species will move either towards an internal equilibrium point $(0 < p < 1)$ or near extinction $(p \approx 0)$, with the latter occuring less frequently than the former. Thus many species under this scheme will again produce a more or less uniform (random) frequency distribution of species occupying different proportions of available sites, possibly with a slight peak at $p \approx 0$ which may or may not
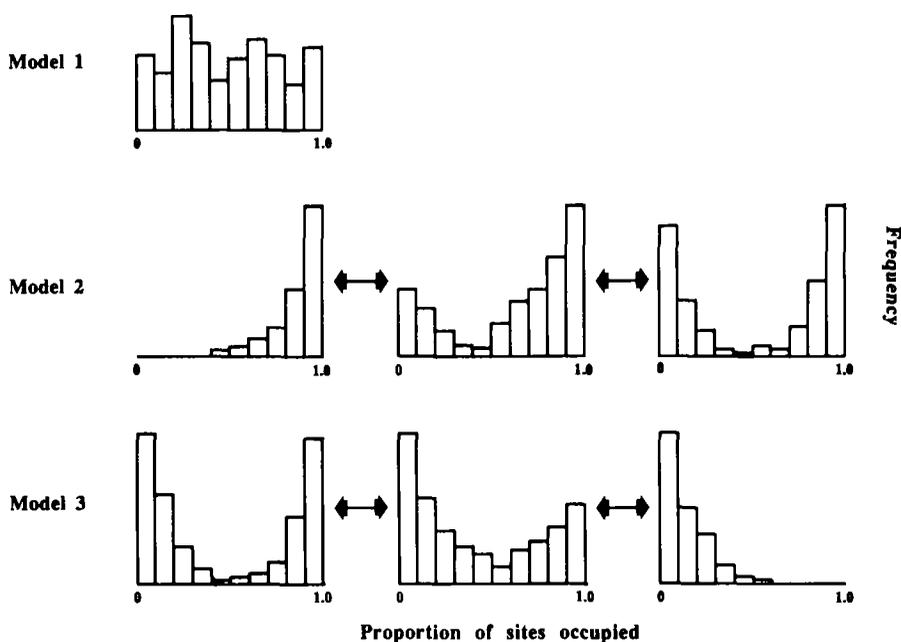

Fig. 2. Contrasting patterns of modality in spatial occupancy expected from three models of spatial dynamics. Model predicts uniform/random frequency distribution. Model 2 ranges from single modality with a mode at $p \approx 1$ (left graph) to bimodality with the second (weaker) mode at $p \approx 0$ (middle and right). Model 3 ranges from bimodality with nearly equal modes at $p \approx 0$ and $p \approx 1$ (left) through the reduced mode at $p \approx 1$ (middle) to single modality at $p \approx 0$ (right). See THEORY, "Assumptions and predictions".

be distinguishable from other peaks occuring haphazardly. In model 3 the case (ii) makes the probability of becoming rare ($p \rightarrow 0$) much higher than that of becoming wide-spread ($p \rightarrow 1$) as a result of an increased occurrence of $i < e$. $p = 1$ is not necessarily a stable equilibrium point, because negative values of dp/dt invariably occur from time to time due to stochastic variation in i and e, leading to a decrease in p. Furthermore if p drops under e/i in this process, its approach to $p \approx 0$ will be more accelerated. In other words, p is unlikely to increase in value when it is already small because of the joint operation of $i < e$ and $0 < p < e/i$ which both induce a decline in p, whereas there is no guarantee of large p (≈ 1) maintaining its value for a long period of time. Thus, many species following the dynamics of model 3 under case (ii) will ultimately produce a frequency distribution with a single, large mode at $p \approx 0$ (Fig. 2, model 3, right), which corresponds to an abundance of rare species in a community

It is notable here that only in model 3 the magnitude of p has any bearing upon the final pattern of modality. In model 2, p has no influence on the outcome which is entirely decided by the relative magnitude of parameters i and e. Similarly, the values of i and e completely determine the behaviour of model 1, where $p \rightarrow 0$ for $i < e$ and $p \rightarrow (i - e)/i$ for $i > e$. Assuming that the case (ii) is applicable with more reality than the case (i), the dynamic behaviours of these three models can be summarised as follows (Fig. 2). Model 1 predicts a uniform (random) frequency distribution of species with respect to the proportion of sites occupied. Model 2 predicts either single modality with a mode at $p \approx 1$ or bimodality with modes at $p \approx 0$ and $p \approx 1$, the latter mode being always larger than (or equal to, if $r = 0$ is included in Eq. 4) the former. However, bimodality in this case only occurs with substantial stochasticity incorporated in $(i - e)$. Thus, bimodality in model 2 is unseparable from the phenomenon of 'core-satellite switching', i.e., constant change in the species' status of abundance from rare to common and common to rare. Model 3 predicts single modality with a mode at $p \approx 0$, or bimodality with a second, weaker mode at $p \approx 1$. In contrast to model 2, while switch from core to satellite status ('population crash' over generations) is expected to occur to some extent, the reversal (from satelite to core status) is highly unlikely, though not totally impossible, in this model. If it is assumed that the case (i) is applicable to some communities on some occasions, model 3 may also predict symmetrical bimodality (i.e., modes at $p \approx 0$ and 1 being of the same magnitude), whereas predictions under case (i) for models 1 and 2 are already being included in the predictions under case (ii). Note that symmetrical bimodality could be derived from either model 2 or 3.

Alternative Core-Satellite Model

In an attempt to improve on the core-satellite hypothesis, Hanski (1991a) proposed another model:

$$dp/dt = ip(1-p) - ee^{-\alpha p}p^{1+\tau}. \qquad (5)$$

Note that this model (hereafter called model 4) has four parameters, in contrast to two in models 1, 2 and 3. Parameter i for the immigration rate is the same as in three earlier models. The extinction rate, however, is now influenced by three parameters e, a and τ. Hanski (1991a) states that Eq. (5) produces a bimodal distribution of p values as a stable equilibrium distribution, thus eliminating the issue of core-satellite switching which forms the basis of model 2 as described above but has been found to be seemingly uncommon in nature. At the same time Eq. (5) incorporates the idea of habitat heterogeneity, i.e., variability among habitat units to be occupied, which is not considered in models 1, 2 and 3. Despite this, Hanski (1991a) did not clearly specify parameter combinations which lead to bimodal patterns and it is difficult to define this four-parameter model without specific assumptions. Therefore, no further re-interpretation of this model is attempted in the present study and the model is simply taken to predict bimodality in p without the need for core-satellite switching, as has been suggested by Hanski (1991a). Because the relative magnitudes of the left-most and the right-most class cannot be assessed here, any bimodality (but no single-modality) is accepted as conforming to the prediction of model 4 in the following analysis. If anything, this would have an effect of increasing the chance of model 4 being accepted as an explanation of observed patterns.

Other Models

While models 1 to 4 possess the identical structure with respect to the rate of immigration, i.e., $ip(1-p)$, Gotelli (1991) proposed an alternative structure for models 1 and 2. He assumed that the rate of immigration is dependent only on the proportion of unoccupied sites $(1-p)$, which amounts to constant and random colonization of individuals from an invariable source pool ('propagule rain'). Replacing the first term of Eqs. (1) and (2) with $i(1-p)$,

$$dp/dt = i(1-p) - ep \tag{6}$$
$$dp/dt = i(1-p) - ep(1-p) . \tag{7}$$

These models possess a single internal equilibrium point, $p = i/(i+e)$ and $p = i/e$ for Eqs. (6) and (7), respectively. In the absence of further specifications about the values of i and e, these models as applied to an assemblage of species are considered to behave in the same manner as Levin's original model 1, i.e., uniform frequency distribution of species with respect habitat occupancy. Thus, in testing modality patterns these models are indistinguishable from model 1 and in the following analysis they are subsumed in model 1.

Problems of Extrapolating from Single-Species to Multi-Species Patterns

One difficulty of inferring community-wide patterns of distribution from models treated here which basically refer to a single-species situation is that, the resultant

frequency distributions of habitat occupancy are influenced by probability distributions of parameters i and e which may vary in an unknown manner from one species to another within a community and between different communities. For example, if values of e/i are clustered around certain value for an assemblage of species in a community, a unimodal pattern of frequency distribution will result from model 1 (c.f., Collins and Glenn, 1991). In the absence of information on the probability distributions of i and e across species, the present study follows earlier analyses by Hanski (1982a) and Gotelli and Simberloff (1987) where, essentially, uniform random distributions of i and e among different species within a community were implicitly assumed. Modality predictions as described above are all based on this assumption, apart from restraints considered for values of i and e within a species. With the current state of knowledge this is perhaps the most reasonable approach, especially where a variety of communities are dealt with. Clearly, further research is required for a better understanding of this issue.

ANALYSIS

Modality Testing

It is apparent from the previous section that in analysing real data different patterns of modality in frequency distribution—random (uniform), unimodal and bimodal—need to be distinguished. In the present context the magnitudes of two extreme classes in a frequency distribution, i.e., the left-most class ($p \approx 0$) and the right-most class ($p \approx 1$), are vitally important in seeking correspondence with theoretical predictions. Bimodality, however, is not a purely objective, straightforward statistic but requires a subtle value judgement and definition, the point that has not fully been adressed in previous works testing Hanski's model and thus contributed in part to somewhat conflicting results. Furthermore, failure to recognize the importance of distinguishing a unimodal as against a bimodal pattern in theory and in data analysis seems to have exacerbated the problem of testing modality. For example, Hanski's (1982b) method of applying a χ^2 test for agreement with random (uniform) frequency distribution to pooled data (the left-most class (L1) combined with the right-most class (R1), the second left-most class (L2) combined with the second right-most class (R2), L3 + R3, etc.) does not separate a bimodal pattern from a single-modal pattern; L1 + R1 is large as long as either L1 or R1, not necessarily both, is large. Similarly, Gaston and Lawton's (1990) method of comparing an observed frequency distribution with simulated, randomized data using a χ^2 test does not specify the nature of departure from a random pattern, whether unimodal, bimodal or something else, thus necessitating an ad hoc note based on 'visual' inspection (see table 4 of Gaston and Lawton 1990). Another problem arising from a straightforward comparison between an observed frequency distribution with a random pattern can be illustrated in the following example. The pattern shown in
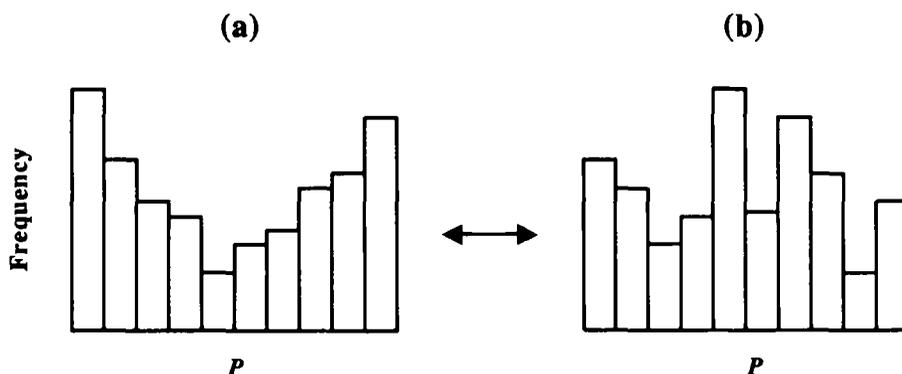
Fig. 3. Example of two different patterns of modality arising from different arrangement of the same constituent frequency values.

Fig. 3a, though 'apparently' bimodal, will not be judged as being different from a random pattern on the basis of a simple χ^2 test ($\chi^2 = 14.5$, d.f. $= 9$, $P > 0.05$) because it is mixed up with a pattern such as in Fig. 3b consisting of the same values of frequency but arranged in a different manner. However, when the arrangement of different frequency classes is taken into account, it is easy to recognize that the pattern represented in Fig. 3a constitutes a very small subset of all the possible patterns, the majority of which looking somewhat similar to Fig. 3b with no clear modes in boundary classes. Thus, in addition to the absolute magnitudes of the left-most and the right-most class, it is also important to consider the general shape of a distribution.

In the light of these, a new, exact probability method for detecting modality trends was introduced, which can be flexibly applied to a range of ecological data encountered. The method was used as a convenient means of defining and recognizing modality patterns in the context of distribution dynamics, rather than as a statistically neutral, foolproof test procedure; some compromise is necessary between ecological relevance and statistical exactness in this matter. Because of the importance of detecting relevant modality trends whenever they occur, errors of Type I rather than of Type II were preferred in the following significance testing. The method takes into account the total number of sites sampled, number of individuals and the interval of frequency classes chosen. First, the sum of probabilities of obtaining the observed frequencies of the left-most (n_l) and the right-most class (n_r) plus more extreme cases (i.e., equal or higher frequencies in the two terminal classes than the observed, both $\geq n_l$ and $\geq n_r$), under a null hypothesis of the random occurrence of species in terms of spatial occupancy, is given as,

$$P_c = \sum_{i=n_l}^{N-n_r} \sum_{j=n_r}^{N-i} \frac{N! h^{i+j}(1-2h)^{N-i-j}}{i!\, j!\, (N-i-j)!} \tag{8}$$

where N is the total number of species and h the class interval ($0 < h < 1$). Furthermore, the probability of obtaining the observed value of frequency for the

left/right-most class plus more extreme cases under the same null hypothesis can be separately calculated as

$$P_l = \sum_{i=n_l}^{N} \binom{N}{i} h^i (1-h)^{N-i} \tag{9a}$$

$$P_r = \sum_{i=n_r}^{N} \binom{N}{i} h^i (1-h)^{N-i} \tag{9b}$$

In assessing modality, $P_c < 0.05$ was employed as a first criterion to separate a significantly single/bi-modal pattern with respect to the boundary classes from other patterns. When in doubt different values of the class interval h were used to lump classes (e.g., L1(R1)+L2(R2), etc., especially when L2(R2) was larger than L1(R1), or smaller but still of substantial magnitude) to ensure that no modality trend is missed simply because of a particular way the frequency distribution is organized; this procedure was necessary because class intervals were not predetermined in most of the data sets. If $P_c < 0.05$ was met, values of P_l and P_r were then used to separate bimodality from single-modality with different grades of single/bi-modality being recognized (Table 1); this classification scheme covers a range of conceivable patterns relevant to the theory of distribution dynamics (Fig. 4). Here, in addition to the calculation of P_c, P_l and P_r, another condition was introduced to separate a very weak bimodality (case 4 of Table 1, Fig. 4d) which may otherwise be classified as (strongly) single-modal (cases 6 and 7, Fig. 4f, g). When one of the boundary classes is judged to be significantly large but the other not (i.e., $\min(P_l, P_r) < 0.05$ and $\max(P_l, P_r) > 0.05$),

Table 1. Classification of distribution patterns in communities

	P_c	P_l	P_r	$t^{[!]}$	Diagnosis[!!]
Case 1	*	*	*	—	strongly bimodal (L or R)
Case 2	*	<0.25	<0.25	—	bimodal (L or R)
Case 3	*	<0.5	<0.5	—	weakly bimodal (L or R)
Case 4	*	*	≥0.5	Y	weakly bimodal (L)
	*	≥0.5	*	Y	weakly bimodal (R)
Case 5	*	<0.5	≥0.5	—	weakly single-modal (L)
	*	≥0.5	<0.5	—	weakly single-modal (R)
Case 6	*	*	≥0.5	N	single-modal (L)
	*	≥0.5	*	N	single-modal (R)
Case 7	*	*	>0.95	N	strongly single-modal (L)
	*	>0.95	*	N	strongly single-modal (R)
Case 8	NS	NS	NS	—	uniform/other

P_c, P_l and P_r refer to probability values (see text for formulae).
* $P < 0.05$ (inclusive of $P < 0.01$ and $P < 0.001$); NS, $P > 0.05$
[!] Existence of t consecutive frequency classes adjacent to the smaller of the left/righ-most class satisfying $(1-\max(P_l, P_r))^{t-1} < 0.05$: Y-yes, N-no.
[!!] L and R indicate the position of the largest mode (α-mode) in a frequency distribution: L, left-most class; R, right-most class.

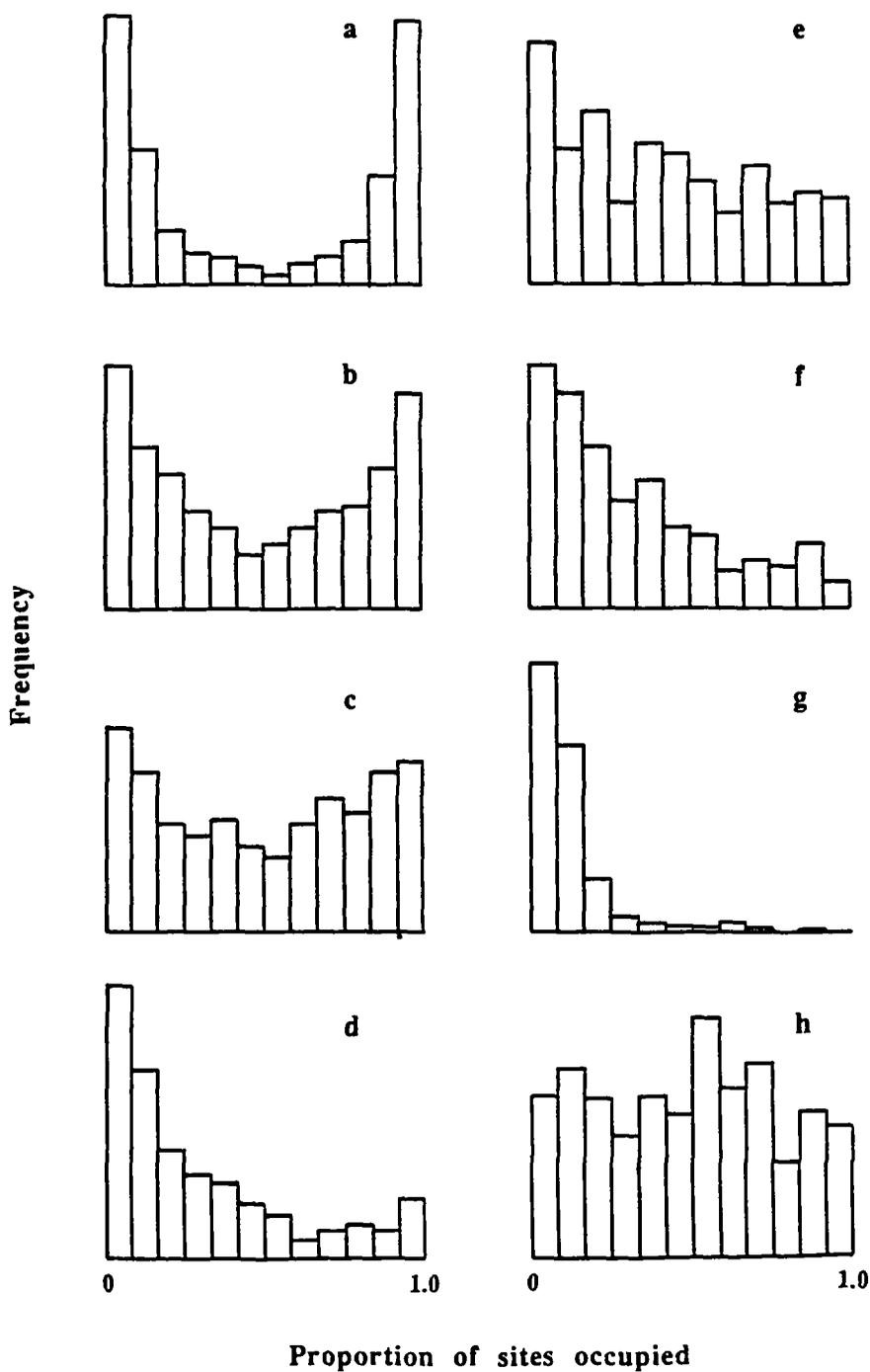Fig. 4. A range of modality patterns relevant to the analysis of distribution dynamics in ecological communities. See table 1 for definition of each pattern. *a*, strongly bimodal (case 1 of table 1); *b*, bimodal (case 2); *c*, weakly bimodal (case 3); *d*, weakly bimodal (case 4); *e*, weakly single-modal (case 5); *f*, single-modal (case 6); *g*, strongly single-modal (case 7); *h*, uniform/other (case 8).

the relative magnitude of the smaller of the two (the one associated with larger probability P_l or P_r) within its neighbourhood classes was assessed on the basis of the formula,

$$[1 - \max(P_l,\ P_r)]^{t-1} < 0.05 .\tag{10}$$

If there exist t consecutive classes adjacent to and smaller than the boundary class in question that satisfy Eq. 10, the boundary class was judged to be significantly large locally and therefore the pattern was denominated as weakly-bimodal (case 4, Fig. 4d) rather than single-modal (case 6) or strongly single-modal (case 7). Note that distinctions between and within single/bi-modality are inevitably somewhat artificial, as any statistical boundary such as $P=0.05$ is. The classification scheme adopted here is partly intended to bias towards recognizing bimodality (i.e., Type 1 error) so that cases of bimodality which has been the focus of core-satellite debate are not underestimated; if it is not detected in this procedure, it is unlikely to be significant under any test. Notwithstanding these caveats, a finer classification of modality here has an advantage of providing more information on where a given pattern lies within the spectrum, which a simple dichotomous division of single/bi-modality cannot. For example, the pattern depicted in Fig. 3a is associated with $P_c=0.000747$, $P_l=0.0206$, and $P_r=0.0726$ for $h=0.1$, thus classified as bimodal (case 2), while the pattern in Fig. 3b is classified as random/other ($P_c=0.188$, $P_l=0.297$ and $P_r=0.679$).

When a mode occurred in an intermediate frequency class its significance was examined using the same formula as P_l or P_r, thus,

$$P_m = \sum_{i=n_m}^{N} \binom{N}{i} h^i (1-h)^{N-i} .\tag{11}$$

where n_m is the observed frequency of class m. In connection with modality analysis, the position of the largest mode (termed as α-mode) in a frequency distribution was also noted.

Data

Published data on animal communities were reanalysed in the light of the present study. In addition, new data on a freshwater chironomid community were also put to the same analysis. Altogether, a total of 56 data sets were analysed with respect to modality patterns and general conformity with theoretical expectations from four models.

RESULTS

Among seventeen data concerning an assemblage of epiphytic chironomids (Table 2), six demonstrated patterns indistinguishable from randomness (U), whilst eight were classified either as single-modal (S) or as weakly single-modal (WS); only

three were bimodal (B)/weakly bimodal (WB) with equal frequencies in the two boundary classes (i.e., α-mode being indicated as L-R, Table 2) or a higher frequency in the left-most than the right-most class (α-mode, L). The position of α-mode was fairly variable among data, over half of them being located in the left-most class while in four data it was equally shared by the left- and the right-most class (L-R). In terms of conformity with predictions from four models, six data (those diagnosed as U) agree with model 1, four (WS/R, WB/L-R and B/L-R) with model 2, nine (S/L, WS/L, WB/L, WB/L-R and B/L-R) with model 3 and three (WB/L, WB/L-R and B/L-R) with model 4. However, the presence of uniform/random patterns in these data may be due to a relatively small number of species involved in each frequency distribution, whilst the underlying trend is that of model 3.

Of the seventeen data concerning the distributions of bracken herbivores (Gaston and Lawton, 1989), eight showed strongly-single modal (SS) patterns with α-mode invariably located in the left-most class. Seven data were classified as uniform/random with α-mode either in the left-most class or in an intermediate class. In contrast to their original analysis (c.f., Table 4 of Gaston and Lawton, 1989), two data concerning 100 km squares were diagnosed as weakly bimodal in the present analysis. However, their conclusion that the core-satellite hypothesis cannot be supported by these data can still be upheld; none of the data conformed to expectations of model 2 (i.e., single- or bimodality with R larger than L), only two data (WB/L) agreed with model 4, whereas all of the significant departures from randomness (ten among seventeen) are in agreement with model 3. As with the epiphytic chironomid data, the reason for a high proportion of data being diagnosed as uniform/random patterns may relate to a relatively small number of species (≤ 20) comprising each assemblage, thus obscuring patterns.

Data on bumblebees present a mixed picture. Four out of ten data showed bimodality, two of them having the right-most class as α-mode; these were the only data in agreement with the original core-satellite hypothesis in the strict sense (i.e., σ_r^2 substantially larger than $\bar{r}$ in Eq. 4, see MODELS). Four data diagnosed as single-modal had α-mode in the left-most class. Thus, two data (U) conform to model 1, two (B/R) to model 2, six (WB/L and S/L) to model 3 and four (B/R, WB/L) to model 4.

Other miscellaneous communities covered a spectrum of patterns ranging from bimodal (island insects and *Onthophagus* beetles) to strongly single-modal (soil mites, crustacean zooplankton and helminth parasites in eels), all of them having α-mode in the left-most class except one (*Onthophagus* beetles where L and R are of equal magnitude). All of these 12 data sets agree with model 3 while none conforms to model 1, only one (B/L-R) to model 2 and six (B/L, B/L-R and WB/L) to model 4.

For animal communities as a whole, the proportion of data conforming to each of the four models is 26.8% (15 data) for model 1, 12.5% (7 data) for model 2, 66.1% (37 data) for model 3 and 26.8% (15 data) for model 4.

Table 2. Patterns of spatial distribution in animal communities

Community	h	P_c	P_l	P_r	$t^|$	Diagnosis[+]	α-mode[!!]
Epiphytic chironomids[1]							
March 1983	0.2	**	*	0.802	N	S	L
April	0.2	NS	0.161	0.678	N	U	L
May	0.2	*	0.161	0.383	N	WB	L
June	0.2	NS	0.203	0.497	N	U	L
July	0.2	NS	0.423	0.790	N	U	I
August	0.2	**	**	0.866	N	S	L
September	0.2	***	***	0.893	N	S	L
October	0.2	*	*	0.790	N	S	L
November	0.2	*	0.0504	0.914	N	WS	L
December	0.2	*	0.262	0.262	N	WB	L-R
January 1984	0.2	NS	0.322	0.322	N	U	L-R
February	0.2	NS	0.383	0.383	N	U	L-R
March	0.2	*	0.678	0.0504	N	WS	R
April	0.2	*	0.0504	0.678	N	WS	L
May	0.2	NS	0.832	0.203	N	U	I-R
June	0.2	*	0.832	0.0563	N	WS	R
July	0.2	*	0.203	0.203	N	B	L-R
Bracken insects[2]							
All sites	0.1	**	**	>0.999	N	SS	L
May	0.1	***	***	>0.999	N	SS	L
June	0.1	*	*	>0.999	N	SS	I[a]
July	0.1	NS	0.323	>0.999	N	U	I
August	0.1	**	**	>0.999	N	SS	L
September	0.1	NS	0.415	0.771	N	U	I
Unshaded sites	0.1	NS	0.0522	>0.999	N	U	L
Lightly shaded	0.1	**	**	>0.999	N	SS	L
Shaded	0.1	***	***	>0.999	N	SS	L
10,000 km² squares (i)	0.2	NS	0.690	0.690	N	U	I
(ii)	0.2	NS	0.383	0.914	N	U	L-I
(iii)	0.2	**	**	>0.95	N	SS	L
(iv)	0.2	*	*	>0.99	N	SS	L
100 km² squares (i)	0.2	*	0.161	0.383	N	WB	L
(ii)	0.2	NS	0.121	0.624	N	U	L
(iii)	0.2	NS	0.263	0.672	N	U	L
(iv)	0.2	**	*	0.423	N	WB	L
Bumblebees							
Lublin, Poland[3]	0.167	***	0.232	**	N	B[b]	R
Southern England[4]	0.2	***	**	0.402	N	WB[c]	L
S-E England[5] (i)	0.167	*	*	>0.999	N	S[d]	L
(ii)	0.167	***	0.158	*	N	B	R
(iii)	0.167	**	*	0.513	N	S	L
Northern England[4]	0.143	*	*	0.573	N	S	L
Scotland[4]	0.2	NS	0.383	0.678	N	U	I
Southern Ireland[4]	0.2	*	*	0.931	N	S	L
Southern Sweden[6]	0.222	NS	0.419	0.232	N	U	R
Islands of Britain[4]	0.2	***	**	0.352	N	WB	L
Miscellaneous communities							
Insects on mangrove islands[7]	0.1	***	***	0.0886	N	B	L
Onthophagus beetles[8]	0.167	*	0.168	0.168	N	B	L-R
Soil mites (i)	0.1	***	***	0.730	Y	WB	L
(ii)	0.1	***	***	>0.99	N	SS	L
Crustacean zooplankton (i)[10]	0.1	**	**	0.948	N	S	L
(ii)[11]	0.1	***	***	>0.999	N	SS	L
Helminths in ducks[12]	0.111	***	***	0.844	Y	WB[e]	L
Helminths in rockfish[13]	0.125	***	***	0.442	Y	WB	L
Helminths in eels[14] (i)	0.1	***	***	>0.999	N	SS	L
(ii)	0.1	***	***	>0.999	N	SS	L
Desert rodents[15]	0.167	*	*	0.619	N	S	L
Songbirds[16]	0.2	**	0.0561	0.267	N	WB	L

<center>DISCUSSION</center>

Model Testing

With models considered as stochastic versions of eqns 1–3, there are three cases behind an unsuccesful fit of a model to data: (i) the basic, deterministic model is correct, but a stochasticity assumption adopted is incorrect; (ii) the basic model is incorrect but the stochasticity assumption is correct; (iii) both the basic model and the stochasticity assumption are incorrect. On the other hand, if a particular data set did not conform to a model, it is in theory possible to claim that the data did not satisfy a more fundamental assumption of the model, e.g., habitat homogeneity as mentioned above; in that case, the model may not totally be invalidated. However, it is perhaps more important to recognize that if no or very few data among many agree with the expectations of a model, that model must embody inappropriate assumptions and/or constitute a poor representation of the phenomena prevailing in nature; it will then be logical to conclude that the model on the whole is fundamentally unrealistic with respect to the ecological phenomena under consideration. This point needs to be taken into account in comparing different models.

One of the assumptions which may be linked to most models treated here is that, as Hanski (1982a, b) emphasized with reference to his core-satellite hypothesis, all the sites under consideration are equally available for colonization by all the species in the community; in other words, habitat is regarded as more or less homogeneous. Indeed Hanski (1982a) stressed that this should at least approximately be confirmed before model 2 is tested. However, if a species is absent from a particular site in nature, there is no way of knowing whether the site is as equally colonizable as other sites already colonized; an experimental confirmation of a large number of such empty sites

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Data: *1*, this study; *2*, Gaston and Lawton (1989); *3*, Anasiewicz (1971); *4*, Alford (1975); *5*, Williams (1988), (i)—2 km grid squares ($n=450$), (ii)—2 km grid squares ($n=20$), (iii)—10 km grid squares ($n=410$); *6*, Løken (1973); *7*, Simberloff (1976); *8*, Hanski (1982a); *9*, Karppinen (1958), (i) and (ii) refer to communities from different soil types; *10*, Patalas (1971); *11*, Rigler and Langford (1967); *12*, Table 1 of Bush and Holmes (1986), frequency data presented in fig. 2 of this reference do not exactly match those of Table 1; *13*, Holmes (1990); *14*, Kennedy (1990), (i)—geographical occurrence ('component community') in the British Isles, (ii)—occurrence in individual eels ('infracommunity'); *15*, Brown (1984); *16*, Bock and Lepthien (1976) and Bock and Ricklefs (1983), for 22 endemic species of subfamilies Emberizinae and Carduelinae.

h, class interval in frequency distributions; P_c, P_l and P_r, probability values (see text for formulae). NS, $P>0.05$; *, $P<0.05$; **, $P<0.01$; ***, $P<0.001$.

! Existence of *t* consecutive frequency classes adjacent to the smaller of the left/righ-most class satisfying $(1-\max (P_l,\ P_r))^{t-1}<0.05$: N-no, Y-yes.

+ Diagnosis: SB, strongly bimodal; B, bimodal; WB, weakly bimodal; SS, strongly single-modal; S, single modal; WS, weakly single-modal; U, uniform/other.

!! Position of the largest mode: L, left-most; R, right-most; I, intermediate.

a, referring to the second left-most class; the left-most class has a second largest frequency.

b, diagnosed as WS (mode=L) when analysed with 10 sites and $h=0.1$

c, diagnosed as S (mode=L) when analysed with $h=0.1$

d, a second mode of some significance ($P=0.158$) exists in an intermediate class.

e, trimodality, as claimed by original authors, does not exist with $h=0.111$. With $h=0.0666$ the third mode appears but cannot be judged to constitute a significantly distinct mode in the present analysis.

in the field is almost out of question. Furthermore, this assumption of homogeneity is conceptually at odds with another of Hanski's views that his model considers a wider, geographic distribution of species ('distribution', c.f., Hanski, 1982a), not a small scale distribution within a community ('frequency') as envisaged by Launkiaer (1918). It is hardly possible to expect that habitat sites over a geographical area of distribution of any species are all of equal value for colonizing individuals. Thus the assumption of homogeneity and the view that a model refers to the geographical distribution of species *cannot strictly be taken together in considering these models*. In view of this the most reasonable approach is to adopt a less strict interpretation of habitat homogeneity whilst choosing an area of habitat not overtly heterogeneous for an assemblage of species under study. If this is accepted, there is no reason to reject data sets such as those on freshwater chironomids and bracken herbivores (Table 2) on the ground of habitat homogeneity or scale of distribution considered; these encompass no less homogeneous habitats than the data analysed by Hanski (1982a, b, c).

Gotelli and Simberloff (1987) argued that the plant community data for separate soil types were significantly more bimodal than all the data combined, thus in effect using the sum of data as a null condition against which to test modality; a reverse approach was taken by Collins and Glenn (1990) to compare large, regional distributions with what was expected from averages of watersheds within a region. However, the real 'null' condition implicit in these models is that, originally, any species can occupy any proportion p of sites available; then the models describe different patterns of spatial dynamics through time. In other words these models depict spatial processes against the background of evolutionary stochasticity and possibilities, not against any present-day configuration of a community. From this perspective the exact probability method adopted in this work seems more appropriate for assessing modality in community data.

Why Bimodality?

Very loose interpretations of 'bimodality' seem to have exacerbated the analyses of data in connection with the core-satellite hypothesis, where bimodality has been taken to include everything with a minimum of peaks in boundary classes in a frequency distribution. As has been shown in the section on THEORY, it is important to recognize that a) bimodality in model 2 is only possible with substantial stochasticity in r, corresponding to a subset of Eq. 4; Eq. 4 itself is not a sufficient condition for bimodality and, b) as long as eqn 4 is assumed, the mode at $p \approx 1$ is expected to be larger than the mode at $p \approx 0$. The fact that only two out of 56 animal community data were diagnosed as bimodal with the α-mode in the right-most class suggests that Hanski's (1982a) original hypothesis is not a realistic proposition for these communities. Moreover, bimodality in general (without specifying the α-mode) occurred in less than a third of the data sets, thus casting doubt on the applicability of Hanski's (1991a) alternative core-satellite model (model 4).

Here it may be worthwhile to consider the core-satellite hypothesis (corresponding to bimodality) separately from more general patterns (single- and bimodality) of model 2; the former constitutes a small subset of the latter. In connection with the earlier discussion of ill-fit of a model, an interesting question is which part of the core-satellite hypothesis is unrealistic, the assumption of high level of stochasticity, the structure of model 2 itself, or both. The assumption of stochasticity is difficult to test independently in a strict sense, because what is needed to measure is temporal variation in the parameters (or alternatively, intrinsic rates) of colonization and extinction ($= i$ and e), rather than any realized rate of colonization or extinction. Roughly, however, this may be translated as 'core-satellite switching', indicating that species change their status from core to satellite and from satellite to core due to a large stochastic variation in the rates of colonization and extinction through time. Unfortunately there is a paucity of long-term data to bear on this aspect, but the few data available tend to show a temporal constancy in abundance status, rather than a wild fluctuation envisaged in the assumption (e.g., plants, Silvertown, 1987; mollusks, Jablonski, 1987; insects, Gaston and Lawton, 1989). Furthermore, no improvement was gained in terms of fitting data by dropping the stochasticity assumption; model 2 could account for only seven out of 56 animal assemblages. Thus the most reasonable conclusion is that both the stochasticity assumption, the hub of the original core-satellite hypothesis, and its parent model 2 are both inadequate descriptions of real communities.

At this point one could still argue that, as long as Eq. 4 is fulfilled, $L > R$ may be expected from time to time due to stochasticity. This may be true. With a large number of data sets, however, $L < R$ should be predominant; this was not the case in the real data. On the other hand, if we assume instead of Eq. 4,

$$\sigma_r^2 > |\bar{r}| \text{ and } \bar{r} < 0 \tag{12}$$

model 2 will predict $L > R$ which conforms to real data. But this assumption is grossly unrealistic in that the parameter (or intrinsic rate) of colonization is supposed to be on average smaller than that of extinction; this is unlikely to apply universally to species in an extant, as opposed to extinct, community. Taken together, there seems little justification for supporting model 2 in any way.

In contrast to model 2 where bimodality is strongly linked to (seemingly unrealistic) core-satellite switching, model 4 depends on habitat heterogeneity to produce bimodality. Thus, model 4 introduces a new dimension to the metapopulation approach where patches have technically been treated as a homogeneous entity. On the other hand, the four-parameter model is elusive in structure and defies a closer examination in the absence of further assumptions. However, if the model is interpreted to predict bimodality in its broadest sense as opposed to single modality, results of the present analysis suggests that the model could at best account for a minority of community patterns. Whilst further analysis of

model 2 does not seem particularly promising, model 4 requires more investigation, especially the consideration of plausible parameter combinations and model behaviours.

Other Explanations?

Bimodality is not constrained to model 2; indeed its derivation from model 2 appears more contrived than that from model 3. As mentioned above, model 4 has also been proposed to account for bimodal frequency distributions. In the light of the present analysis, however, the importance of bimodality as a general phenomenon may be reduced in comparison with the more persistent occurrence of single modality in natural communities (c.f., Gaston and Lawton, 1989). Moreover, the vast majority of bimodality occurred as weakly-bimodal patterns which verge on single-modality. Nevertheless, it is worthwhile to pay attention to explanations other than models examined here to consider bimodal patterns.

Raunkiaer (1918, 1934) suggested that a bimodal pattern may occur due to the presence of species which have the centre of distribution coinciding with the area under study and other species with marginal occurrence. Basically the same explanation was proposed by P. H. Williams (1988) with reference to the distribution of bumblebees. In analysing the geographical distributions of a variety of insects, birds and plants, Hengeveld and Haeck (1982) found that the highest abundances occur near the centre of a species' range and the lowest at the margins. Thus it may be argued that a bimodal pattern results from species of central and marginal distributions within the prescribed sampling area. However, the existence of such heterogeneous distributions does not necessarily lead to bimodality because there is nothing concrete to guarantee that perceived 'central' and 'marginal' species are both more numerous than species of 'intermediate' occurrence within the area under consideration. Indeed the same logic could be employed to suggest unimodality assuming the preponderance of marginal species in any study area; the argument is basically circular and does not answer why marginal/central species are abundant in the first place. This static explanation is therefore too vague to be of general theoretical relevance.

C. B. Williams (1964) and Brown (1984) suggested that bimodality is an artefact of inadequate sampling. With a limited number of sampling units widespread, common species and rare species may be recognized, but as the number of samling units is increased common species decline in number and rare species increase. The size of a sampling unit (quadrat) also affects this process. As with the previous proposition of central/marginal species, this argument does not explain why there should be a dichotomy of common and rare species in the first place, though the effects of increased samples may be reasonable and realistic.

The combination of log (-normal) distribution of species abundance (Fisher et al., 1943; Aitchison and Brown, 1966; Preston, 1948, 1962, 1981; C. B. Williams, 1950; Sugihara, 1980) and random dispersal (Gause, 1936) may produce a bimodal pattern

due to an excess of species with low abundance which are inevitably associated with low habitat occupancy, and species with high abundance which attain $p=1$ as a boundary condition. In this case dispersal (colonization) may not have to follow a strictly random process (as long as it is not excessively skewed or contagious) to lead to bimodality. More significantly, however, depending on the range of abundances realized by an assemblage of species, the resultant pattern may also be unimodal or even uniform. For example, if the range of abundances covers low values over a spectrum, a single mode at $p \approx 0$ only may exist. Similarly if the range of abundances is narrow and represents intermediate values, not extending much towards low/high values, then a uniform pattern of frequency distribution may emerge. Thus this explanation does not specify modality patterns; indeed this may simply be interpreted to emphasize a mechanistic link between abundance and distribution, whilst leaving the dynamics of spatial distribution untouched.

Rare-Majority Paradigm

Notwithstanding the above discussion of bimodal frequency distributions of spatial occurrence, the central issue may not be bimodality but single-modality with an abundance of rare species in a community, which has not apparently been related to a previous model of spatial dynamics. Though Collins and Glenn (1991) interpreted Brown (1984) as predicting a unimodal pattern, this is dependent upon a host of unstated assumptions that are not part of Brown's (1984) original suggestion. It is therefore interesting to note that a simple model (model 3) could account for both unimodal and bimodal patterns widely observed in ecological communities. This does not necessarily mean that mechanisms embodied in model 3 are always appropriate for natural communities, but as far as models treated in this work are concerned model 3 appears parsimonious in structure and yet flexible in explaining observed patterns with a minimum of ad hoc assumptions.

As has been described in THEORY, Levin's (1970) model (model 1) as well as Gotelli's (1991) modification of models 1 and 2 (Eqs. 6 and 7) in deterministic forms possess a single equilibrium point. While a uniform frequency distribution of species in terms of habitat occupancy is predicted on the assumption of uniform random probability distribution of such equilibrium points (p) among members of a community (see THEORY, Problems of extrapolating from single-species to multi-species patterns), values of p may as well be clustered around a certain value which would in turn lead to a single-modal pattern of habitat occupancy. However, this is still insufficient to explain why a single mode occurs in the lowest habitat occupancy class in the majority of cases. Besides, the assumption of 'propagule rain' as Gotelli's (1991) invoked, i.e., unvarying supply of colonizing individuals from outside the system considered, may be too unrealistic even for plant communities with long-lived seed banks, since there is no evidence to suggest that germination (analogous to colonization of a new habitat patch) occurs constantly year after year.

In connection with the core-satellite hypothesis, Nee et al. (1991) suggested that the number of satellite species recorded could be artificially inflated by sampling bias and the inclusion of 'vagrant' or 'tourist' species. Whilst sampling bias is always a possibility, the extent to which this could significantly modify observed patterns in practice is hard to assess; in general the observed mode of rare species is extremely strong (c.f., Gaston and Lawton, 1989) to leave little doubt about its existence. Furthermore, the definition of 'vagrant' species as opposed to rare but 'genuine' members of a community is not at all clear in the context of analysing distribution dynamics in ecological communities. If the problem is more of a semantic nature, it is perhaps better to consider all the species of a supposed community, without artificially excluding certain species as 'vagrants'; they may represent vital components when global patterns of distribution among species are considered.

One pattern which did not seem to fall naturally within the realm of model 3 is bimodality with $L < R$ as seen in some communities of bumblebees and anthropochorous plants. An interesting question is, is this unexplainable under model 3? One feasible suggestion is that as bimodality is being achieved in the process of model 3, some or a good proportion of species in the rare category ($p \approx 0$) may actually go extinct on a regional scale, leading to a reduction in the left-most class (transition from $L > R$ to $L < R$). This is a tantalizing possibility which requires further study. In a wider context, both theoretical developments and rigorous data on a wider range of communities will be vital for a better understanding of the dynamics of spatial distribution; models treated here are still a very crude approximation of the natural world.

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動物群集の分布動態：理論と解析

渡慶次　睦範

動物群集における分布とアバンダンスの動態についての理論的および解析的問題を調べた．分布域内で出現する地点の割合について種数の度数分布を描いてみると，多くの群集では，低いアバンダンスと限られた空間分布をもつ種（すなわち希種）が顕著なピークを示す形に代表される．空間的出現度数の分布における単峰型と双峰型パターンを評価する新しい方法を用いて，いくつかの動物群集データについて，新提案のものを含めて，分布動態のモデルを比較した．データは，多数の希種をもつ単峰型が双峰型よりも多いことを示した．双峰型がみられた場合でも，多くは広い分布をもつ種のピークが希種のそれよりも小さい．したがって，局地的絶滅率がパッチ占有（または個体群アバンダンス）に対して負の関係をもつと仮定した新しいモデルが従来のモデルよりも観察データによく適合する．解析上のいくつかの問題，特にモデルの前提と検定について考察した．