

## NICHE APPORTIONMENT OR RANDOM ASSORTMENT: SPECIES ABUNDANCE PATTERNS REVISITED

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### SUMMARY

(1) This work examines the theoretical framework of species abundance patterns and the practical problems of applying models to real data, with particular reference to communities with a relatively small number of closely related species.

(2) An attempt is made to give logical coherence to a range of niche apportionment models, including some newly developed ones. Niche apportionment can be categorized through the sequential breakage process of total niche, including the MacArthur Broken-Stick model which has traditionally been envisaged as a simultaneous breakage model.

(3) Five niche apportionment models, i.e. Geometric Series, Dominance Preemption, Random Fraction, MacArthur Fraction and Dominance Decay are contrasted to a model where no conventional niche apportionment is assumed, i.e. Random Assortment model which may relate to a highly dynamic community under a variable environment. In addition, Composite model is proposed which combines niche apportionment and random assortment.

(4) Species-abundance data from a community of epiphytic chironomids were used to illustrate the analyses involving the seven models. Random Fraction and Random Assortment both successfully fitted the data based on the number of individuals, whereas only Random Assortment successfully fitted the biomass data. The epiphytic chironomid community is considered to represent a highly dynamic system which is not structured through the process of niche apportionment envisaged here.

(5) Subtleties of analysis involving a model-fitting exercise are discussed.

### INTRODUCTION

The idea that patterns of relative abundance of species reflect some kind of structure in ecological communities has stimulated much theoretical endeavour and empirical attempts to fit models to real data. Species-abundance data being such a basic component of community studies, this research tradition is considered a natural and logical course of development within community ecology. Despite this background, however, there still remains a number of theoretical ambiguities and practical difficulties in the discipline whilst, in recent years, the trend in community ecology has been to pay less attention to a static descriptor such as relative-abundance pattern, concentrating more upon directly unravelling dynamic processes and mechanisms which underlie community organization. However, the question 'Why are species abundance patterns as they are?' remains a valid one and deserves an objective answer, independently of whether these patterns are related to some tangible structure in communities.

One of the ambiguities in the analyses of species abundance relates to the parallel development of statistically-orientated and niche-orientated models in the past and their haphazard application to community data. Whilst statistically orientated models such as

log-series and log-normal model (Fisher, Corbet & Williams 1943; Preston 1948, 1962) have been successfully fitted to a range of data sets, particularly those representing communities with large numbers of species, more often than not these merely serve as a convenient summary statistic of communities and by themselves reveal very little about community structure (see, however, Kempton & Taylor (1974) and Taylor, Kempton & Woiwood (1976), in terms of analysing diversity). In a sense this state of affairs is inevitable, as an assemblage of a large number of species is more likely to represent a heterogeneous mixture of confounding and possibly opposing factors which tend to mask any structure in a community. In this respect, communities with a small number of taxonomically related species are considered amenable to a more meaningful analysis in terms of species-abundance patterns and mechanisms underlying them, for which niche-orientated models may hold more relevance. However, the two well-known niche-orientated models, namely the MacArthur Broken-Stick (MacArthur 1957) and the Geometric Series models (Motomura 1932), both referring to how the total niche of a community represented by a stick should be broken into pieces (i.e. species niche and hence, abundance), are highly idealistic to the point that it is even difficult to draw a sensible ecological analogy (cf. De Vita 1979). Thus, in terms of understanding community structure little can be gained from analyses involving these models, even if a successful fit to data (which in practice has turned out to be very problematic) is achieved.

Nevertheless, the fact that the above four models have repeatedly been highlighted in the ecological literature for over two decades tends to reinforce the impression that these together cover the whole range of possible species-abundance patterns, and that their non-fit to data is more of an indication of some deficiencies or incompleteness on the part of the data concerned, rather than of deficiencies in the theoretical framework. This, in turn, may have led to under-reporting of data not conforming to models, and also to a very limited amount of work being directed towards seeking other theoretical possibilities (e.g. Hughes 1984).

The present study attempts to establish a logical, coherent basis for a range of species-abundance models, including some newly developed ones, and presents an illustrative analysis using data on freshwater chironomids. Emphasis is on niche-orientated models and their ecological implications rather than on statistical models, as the former are more likely to yield information directly pertinent to community structure when applied to communities containing a small number of closely-related species. In particular, attention is focused on different ways in which total niche can be apportioned among constituent species of a community. As is described in the next section, niche apportionment can reasonably be categorized on the basis of successive invasion or carving-out of niche space by species. These niche-apportionment models are then contrasted to models where little or no interaction between species is assumed with respect to niche/resource use, i.e. species-abundance patterns are strongly dictated by more or less random processes. Finally, implications and subtleties of these analyses are discussed, as exemplified by a study on the community organization of chironomids.

## MODELS

If a community consists of species with similar resource requirements and tendencies to interact within the same niche space, the process of niche apportionment among species can be likened to a unit mass or stick being divided into pieces according to some division rules. Traditionally, the Geometric Series model and the MacArthur Broken-Stick model

have been thought to represent two contrasting patterns of such division: 'sequential breakage' and 'simultaneous breakage', respectively (Pielou 1975; Sugihara 1980). However, for the logic presented below, the MacArthur Broken-Stick model can also be described as a sequential breakage model, which would in fact provide a better ecological insight and facilitate a link with other models. Here, for simplicity, the abundance of a species is assumed to correspond directly to the amount of niche apportioned to that species (cf. Whittaker 1977). Thus, five niche-apportionment models are presented here, all based on the sequential breakage process. In addition, a model relating to random assortment (in terms of species abundance) is introduced, which makes a contrast to niche-apportionment models. The seventh model is a hybrid between niche apportionment and random assortment models. In this paper the term 'relative abundance' refers to proportional abundance of a species ( $\leq 1.0$ ) against the combined abundance of all the species in an assemblage, in terms of either number or biomass.

#### *Geometric Series model*

In this model a first species is supposed to preempt a fraction  $k$  of the total niche, a second species  $k$  of the remainder, a third again a fraction  $k$  of what remains after the first and the second species have carved out their shares, and so on. Then the relative abundances of species form a geometric series (Motomura 1932), with the  $i$ th species having a value expressed as;

$$P_i = k(1-k)^{i-1}$$

When only  $n$  most abundant species are considered out of a total of  $s$  ( $> n$ ) species in a community, as is often the case with censused data, the corrected relative abundance for the  $i$ th species takes the form:

$$P_i = \frac{k(1-k)^{i-1}}{1-(1-k)^n}$$

This model is deterministic in the sense that it does not allow any variation in  $P_i$ , once the parameter  $k$  is set. Mathematical treatment of this model is to be found in May (1975) and Pielou (1975) while examples of its application are given in Whittaker (1972, 1975) and McNaughton & Wolf (1970).

#### *Dominance Preemption model*

This model is a more general form of the Geometric Series model. The first species exerts its dominance by preempting more than half the total niche available and leaves the remainder to be exploited by the second species in the same manner, and so on. Note that a fraction ( $k'$ ) to be preempted by successive species could take any value between 0.5 and 1.0 (uniform random). Therefore, this model stresses the dominance hierarchy formed by successive species, rather than the need for different species to exploit the same fraction  $k$  as in the previous model. Dominance of the  $i$ th species is considered absolute in that its abundance exceeds that of all the lower ranking species combined. This is a stochastic model (as are all the models presented here except Geometric Series model) and converges to a GS model with  $k=0.75$  when averaged over many replications, unless further condition is attached to the probability distribution of  $k'$ .

#### *Random Fraction model*

This model envisages niche apportionment as a sequential division of total niche in a random fashion. The niche is first divided at random (uniform) into two fractions, one of

them is then randomly chosen and divided at random (uniform) into further two fractions, thus resulting in three fractions. These three fractions are again subjected to random selection and division to form four fractions, and so on. Note that the Dominance Preemption model is a special case of this model; in the former successive divisions occur exclusively with the smallest fraction, whereas in this model all the fractions, large or small, have an equal chance of being selected for division. In terms of the invasion of niche space by new species, this model is analogous to a situation where a new, invading species randomly selects one of the existing species and gets a random fraction of its niche. In other words, there is no dominance hierarchy among species in this model.

#### *MacArthur Fraction model*

In its original formulation, the Broken-Stick model of MacArthur (1957, 1960) is envisaged as a simultaneous, random breakage of total niche into species niches. In theory,  $n-1$  breakage points are randomly located on a unit stick to create  $n$  fractions. Stated in this way it is difficult to see any relationship between this and other models. However, the same outcome can be obtained through a sequential breakage process. Suppose that a stick is first divided at random (uniform) into two fractions. Then, instead of assuming that the two fractions have an equal chance of being selected for next division (i.e. Random Fraction model), assume that the probability of selection is positively related to the length of each fraction. One of the fractions can thus be selected in a probabilistic manner and subjected to uniform random division to produce two new fractions. Of the three fractions now existing, one can again be chosen depending on the probabilities reflecting fraction lengths, and so on. This process results in exactly the same division principle as the simultaneous breakage approach; breakage points are located randomly over the length of a unit stick. It should be noted, however, that the sequential hypothesis at least leads to a better ecological analogy and more importantly, clarifies its relation with other niche apportionment models. In terms of niche invasion, the model postulates that a new species is more likely to invade the niche space of a more abundant species and gets an arbitrary fraction of it. Under the simultaneous hypothesis, species are assumed to enter the niche arena at the same time and jostle each other to determine each species' niche. In both cases, there is no a priori information on superiority/inferiority among species (but this is not to say that all the species are necessarily assumed to possess the same competitive ability; if so, species would move towards exactly the same level of abundance). The link between this sequential hypothesis and the Random Fraction model is obvious and the difference only refers to how a fraction to be divided or a species to be invaded should be selected. In the latter, the probability of selection is the same for a large and a small fraction, but in the former a large fraction is assigned a higher probability than a small one. Thus, in order to indicate its prototype as well as its closeness to the RF model, this sequential hypothesis is termed the 'MacArthur Fraction model'.

#### *Dominance Decay model*

This model is another species case of the Random Fraction model and is the inverse of the Dominance Preemption model. Instead of picking the smallest fraction of an assemblage for successive divisions, the model stipulates that the largest fraction should exclusively be subjected to division. Therefore, dominance is always negated in this model, whereas the Dominance Preemption model always guarantees it. The model is analogous to a situation where a new species always invades the niche space of the most

abundant species of an existing assemblage. Thus, this model converges towards equitable abundances of constituent species, more strongly than in the MacArthur Fraction model.

#### *Random Assortment model*

This model refers to a situation where abundances of different species are not mutually related at all. This would be conceived of either as a result of non-correspondence between niche apportionment and species abundance, or as a non-hierarchical, dynamic apportionment of niche under a highly variable environment. The former case states that, for reasons such as large stochastic and confounding elements in the processes involved, patterns of species abundance do not reflect underlying niche apportionment among species, whatever form niche apportionment may take. The latter case, which makes no distinction between niche and species abundance (as in all the models mentioned above), can be explained as follows. In a variable environment the total niche of a community does not stay constant in size but experiences a variation through time. Under these circumstances, each species is assumed to carve out its own niche independently of other species in a temporally variable basis. Because of continual change in total niche, species are unlikely to fill up the niche most of the time, though saturation could occur when total niche is contracted or species populations are expanding rapidly. Species niches are also subjected to temporal variation. A major characteristic of this system is that there is hardly enough time for resource-related competitive interactions to develop fully, thus denying the fine-tuning of species niches within a well-defined total niche space.

In a purely theoretical context the model involves a random collection of  $n$  niches of arbitrary sizes. If these niches are ordered in rank from the largest to the smallest, the first, largest niche would be assigned a value of one. Then the second largest niche could by definition take any value less than one. The third would naturally assume a value smaller than that of the second, and so on. Thus, each niche is restricted in size only by its immediate, larger neighbour on the niche-rank axis. This relationship can be expressed as,

$$\begin{cases} N_1 = 1 \\ N_i = r_i N_{i-1} \quad (i \geq 2) \end{cases}$$

where  $N_i$  is the niche size (abundance) of rank  $i$  and  $r_i$  is an independent uniform random variable on  $(0, 1)$ . The expected value of  $N_i$  is given as,

$$E(N_i) = 0.5^{i-1}$$

When an assemblage of  $n$  species is considered, the expected relative abundance ( $P_i$ ) of rank  $i$  is given as,

$$E(P_i) = \frac{0.5^i}{1 - 0.5^n}$$

Therefore, mathematically the model behaves as a stochastic analogue of the Geometric Series model with  $k = 0.5$ .

#### *Composite model*

This model is derived from a consideration that a community of species may encompass two (or perhaps more) separate assembly rules, rather than one only. Probably the most plausible case would be that a few abundant species (e.g. up to the third most abundant in an assemblage) are behaving on the basis of niche apportionment, whilst the rest, less

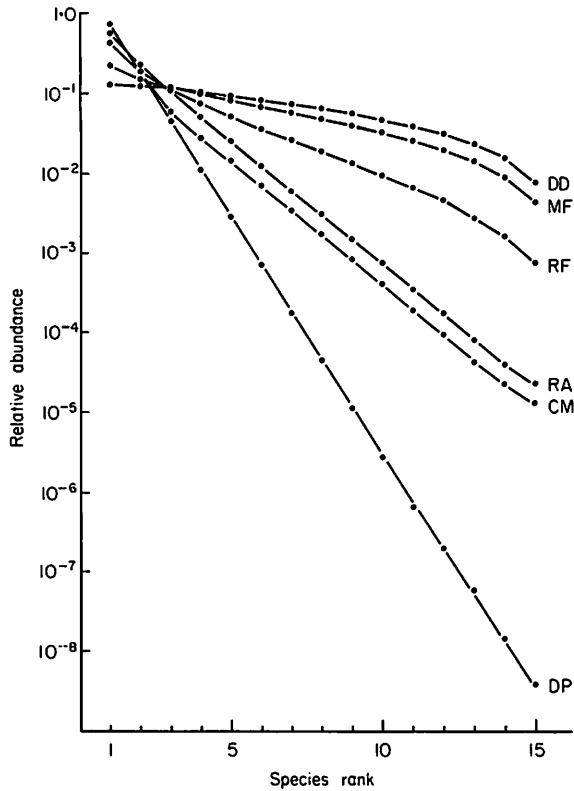


FIG. 1. Rank-abundance patterns of a fifteen-species assemblage expected from six different models: DD, Dominance Decay; MF, MacArthur Fraction; RF, Random Fraction; RA, Random Assortment; CM, Composite; DP, Dominance Preemption. A total of 1000 stimulations were made for each model and relative abundances are expressed as mean values of these replications.

common species, represent a random assortment as envisaged in the previous model. In this case, the model can be built up as a combination of one of the niche apportionment models and the Random Assortment model. If there are only two (abundant) species involved in the first part of this composite model, naturally there would be no difference between GS, DP, RF, MF and DD models; three or more species are required to separate them. However, for small communities such distinction may not be of much importance and a general 'niche apportionment' may be sufficient to describe a situation as against the Random Assortment. In order to institute the Random Assortment model for the second half of a community (i.e. less abundant species), the abundance of the last ranking species in the niche-apportionment group can be assigned a value of unity (one) and the next ranking (i.e. top species of the second group) given a value smaller than this. Subsequent species are assigned with descending values as in the original RA model.

#### *Comparison*

Figure 1 illustrates different patterns of rank abundance demonstrated by these models, except the Geometric Series (which depends on  $k$  to determine its shape), for a community of fifteen species. Within the family of niche-apportionment models the species-

abundance pattern becomes more equitable in the order Dominance Preemption–Random Fraction–MacArthur Fraction–Dominance Decay, reflecting the increasing probability of selection for subsequent division associated with the largest fraction in an assemblage.

## DATA AND ANALYSIS

### *Data*

The data with which the above models of species abundance are compared come from a study on a chironomid community inhabiting a submerged macrophyte, *Myriophyllum spicatum* (L.), in a small river in eastern England. The study site and sampling methods are described in detail in Tokeshi (1985, 1986a, b) and Tokeshi & Townsend (1987); only a brief description is given here. Quantitative samples of apical sections of *M. spicatum* (10 cm in length, where epiphytic chironomids occurred almost exclusively) were taken between March 1983 and July 1984. In the laboratory larvae were sorted individually, identified to species and measured for body length. Biomass of each individual was also estimated on the basis of length–weight relationship obtained for each species (Tokeshi 1986a). Data thus gathered were amalgamated for each sampling occasion (consisting of up to 3000 individuals) to produce species-abundance data in terms of both number of individuals and biomass. A total of thirty-seven such data were put to the present analysis.

### *Analytical basis*

Since all the models except the Geometric Series include stochastic elements, it is meaningless to compare a single example of species abundance obtained from the field to these models. What is important is an average result from many replicated observations, which may or may not come close to the average pattern of species abundance expected from a theoretical model. This aspect of stochasticity has been a major stumbling block in fitting the MacArthur Broken-Stick to real data (Pielou 1975); any meaningful attempt should strictly involve a collection of species-abundance data which contain the same number of species. The same point applies to all the stochastic models presented above. There is also a theoretical dilemma in this attempt. Because niche apportionment models are concerned basically with species of similar taxonomic origin which exploit similar resources, the main thrust of model-testing should involve one type of community alone, not a mixture of diverse communities. However, the requirement for replications in theory means that replicated observations should be mutually independent, implying communities distinct in time and space. Thus, when interpreted literally, these models pose a serious problem of testability.

In order to alleviate this situation the following approach was taken. Species-abundance data pertaining to different sampling occasions were assumed to represent replicated observations of a community dictated by a single assembly rule. Because independency of these data is an important aspect as stated above (although, of course, it cannot perfectly be guaranteed with such data), relatedness of data was assessed with the following formula which quantifies species turnover  $S\tau$  (compositional change of species) from one sample to another (on either temporal or spatial scale):

$$S\tau = 0.5 \sum_{i=1}^n |P_i(t) - P_i(t+1)|$$

where  $P_i(t)$  and  $P_i(t+1)$  denote proportional abundance of species  $i$  in sample (time)  $t$  and  $t+1$ , respectively, and  $n$  is the total number of species occurring on the two occasions. This value ranges from 0 (no change in faunal composition) to 1, (complete change). As shown in Fig. 2, species turnover in terms of both the number of individuals and biomass followed the same pattern, with substantially reduced values (all less than 0.1) between August and February and higher values at other times of year. Therefore, the chironomid community changes very little in species composition during autumn and winter, and species-abundance data taken in this period are considered to be highly related. Thus, for the present analysis, samples taken during spring and summer (March–July, twenty-six in all) were treated as one entity (hereafter called data set A) representing relatively independent, heterogenous replications and contrasted to another entity (data set B, eleven samples, August–February) which was strongly dependent and homogenous internally. For comparison with species-abundance models the data set A is apparently superior and more appropriate; the data set B severely suffers from pseudo-replication. However, for the sake of demonstration both were subjected to the same analysis.

Another point of importance relates to the total number of species treated in the analysis. Because replications should contain the same number of species to make model-testing feasible, and in reality the total number of species fluctuated through time (Tokeshi 1986b), the six most abundant species only on each sampling occasion were treated as a sample assemblage. The decision to take six species into account was made in consideration of the number of replications possible whilst maintaining an assemblage of small but reasonable size which does not significantly depart from reality. Six most abundant species accounted for at least 95% of the total abundance in terms of both number and biomass on each sampling occasion.

#### *Analytical procedures*

For each of Dominance Preemption, Random Fraction, MacArthur Fraction, Dominance Decay, Random Assortment and Composite model, 10 000 simulation runs were performed to create a total of 10 000 six-species assemblages. Using this 'parent population' (consisting of 10 000 items), 95% and 90% confidence limits were derived for mean abundances of the first to the sixth ranking species assuming that a sample of small size ( $n=26$  and 11 items corresponding to the data sets A and B, respectively) was drawn. In other words these C.L.s indicate a range of values of mean abundance for each rank likely to be encountered if a small sample were randomly drawn from the same parent population and mean abundance calculated on the basis of this small sample. With  $\mu_i$  and  $\sigma_i$  denoting, respectively, mean and standard deviation of the abundance of  $i$ th rank in the parent population, the mean abundance value  $\bar{x}_i$  from a sample of size  $n$  is expected to lie within,

$$R(\bar{x}_i) = \mu_i \pm r\sigma_i/\sqrt{n}$$

where  $r=1.96$  for 95% C.L. or  $r=1.65$  for 90% C.L. These theoretical values were then compared with the observed mean abundances derived from data sets A and B. If all the observed values for the first to the sixth rank fell within the corresponding  $R(\bar{x}_i)$  from theory, the observed pattern of species abundance was judged to be in conformity with the model's expectation.

For the deterministic Geometric Series model, values of  $k$  were chosen to minimize the sum of squared Euclidean distance ( $D$ ) between model and observation on a logarithmic scale, thus:



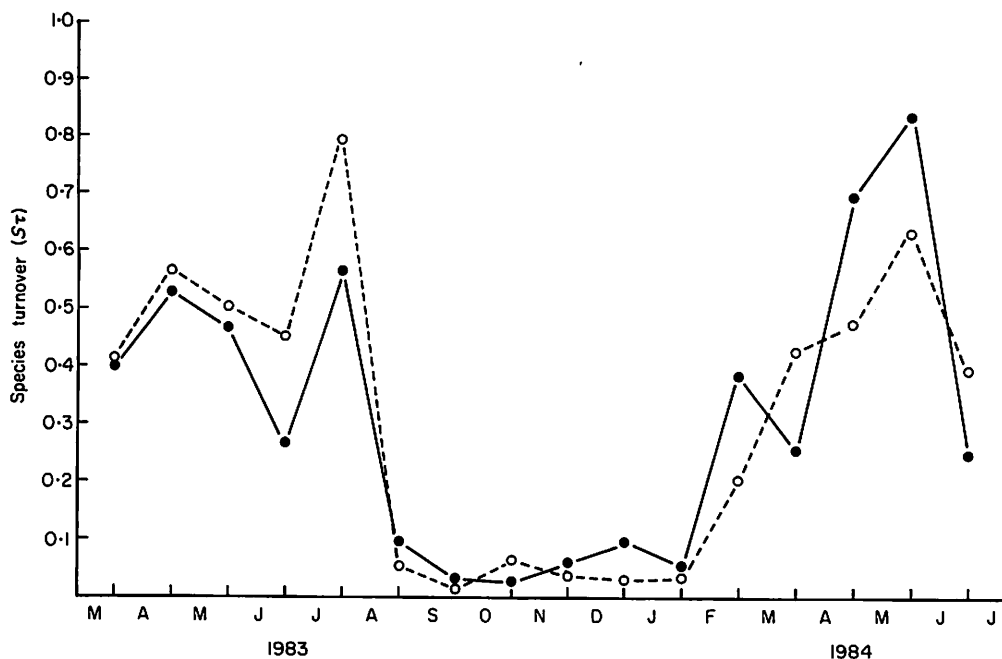


FIG. 2. Species turnover ( $St$ ) in terms of number of individuals (-O-) and biomass (-●-) in the epiphytic chironomid community between March 1983 and July 1984.

$$D = \sum_{i=1}^m [\log P_{\text{obs}}(i) - \log P_{\text{exp}}(i)]^2$$

where  $P_{\text{obs}}(i)$  and  $P_{\text{exp}}(i)$  denote observed and expected abundance of rank  $i$ , respectively, and  $m$  is the number of ranks ( $=6$  in the present study). In line with other stochastic models, this model was fitted to mean abundance data of the data sets A and B. In addition, the model was also applied separately to individual data from single occasions to see the consistency of the result pertaining to mean abundance measures.

## RESULTS

### *Species-abundance pattern: number*

Observed species-abundance patterns in terms of number of individuals, together with seven theoretical patterns, are shown in Fig. 3. For the Geometric Series model, separate versions (different  $k$ ) were fitted to data set A and B. As mentioned in the previous section, the data set B may represent inappropriate replications and indeed bore no resemblance to any of the model expectations. It is therefore excluded from further discussion in this section.

The Geometric Series model with  $k=0.507$  closely approached the observed mean abundance pattern of the data set A, though there is no clear-cut way of visualizing variation around theoretical values of this deterministic model. However, further analysis is carried out later in the section.

The observed pattern of rank abundance for the data set A departed significantly from the Dominance Preemption model towards a more equitable situation, whereas the trend

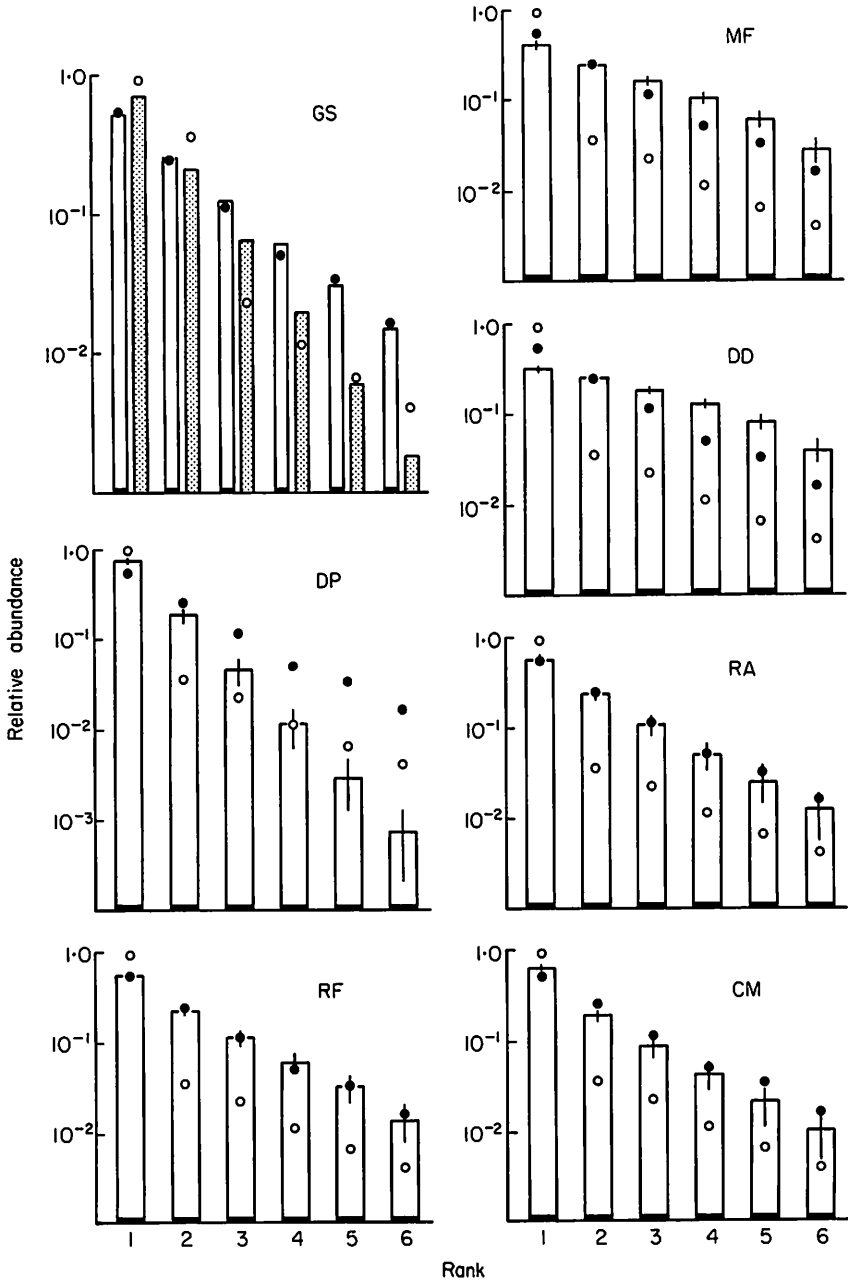


FIG. 3. Patterns of relative abundance derived from seven different models (shown as histograms) compared with observed pattern (●, data set A; ○, data set B; data based on the number of individuals). GS, Geometric Series; DP, Dominance Preemption; RF, Random Fraction; MF, MacArthur Fraction; DD, Dominance Decay; RA, Random Assortment; CM, Composite. In the case of Geometric Series, the model was fitted separately to data set A (□) and B (■). Vertical lines associated with histograms are expected 95% C.L. for mean abundance values corresponding to data set A (see text for detail). C.L. for data set B are excluded here because none of the models fitted the data.

was in the opposite direction with reference to the MacArthur Fraction and the Dominance Decay model. The majority of observed values fell outside the theoretical 95% C.L. of these models, indicating that the models constitute unsatisfactory explanations for the observed pattern. Interestingly, one of the niche apportionment models, i.e. Random Fraction, and the conceptually different Random Assortment model both fitted the data well with all the observed abundance values lying inside the 95% C.L.

In the case of the Composite model it was assumed that the first and the second ranking species apportioned niche between them and the rest followed the Random Assortment model; a three-species version of niche apportionment was also considered but proved to be less satisfactory than the two-species version. Despite closeness at first sight between model and observation, three out of six observed values (the first, second, and fifth rank) fell outside the 95% C.L. and two of the remaining three (the third and the sixth rank) lay within the 95% C.L. but outside the 90% C.L. (corresponding to probability  $0.05 < P < 0.1$  of occurrence). Thus the model cannot be considered to explain the observed pattern successfully.

#### *Species-abundance pattern: biomass*

Figure 4 shows the observed patterns of species abundance in terms of biomass and the patterns derived from seven theoretical models. As with the numerical data, the data set B demonstrated a poor fit to the models so it is excluded from further discussion here.

The Geometric Series model with  $k = 0.561$  resembled the observed pattern of the data set A reasonably well, although this time the discrepancy between model and observation was slightly larger ( $D = 0.100$ ) than in the case with the numerical data ( $D = 0.0655$ ). For Dominance Preemption, MacArthur Fraction and Dominance Decay models, relationships between the observed pattern and the theoretical expectations were exactly the same as in the numerical data. The observed pattern was more equitable than the Dominance Preemption and less equitable than both the MacArthur Fraction and the Dominance Decay model.

The Random Fraction model which demonstrated a good fit to the numerical data did not do so with the biomass data. Observed mean abundance values for the third and the fourth rank were both outside the theoretical 95%, C.L., whilst the fifth rank was barely within the limit (probability  $0.05 < P < 0.10$  of expected occurrence). On the other hand, a perfect fit was again achieved by the Random Assortment model. Observed values for all the ranks were within the corresponding 95% C.L. expected from the model. Finally, a good but not perfect fit was obtained for Composite model incorporating two-species niche apportionment. Only the observed second rank had a mean abundance outside the 95% C.L. and the rest were all within. However, because this model is in a sense a variant of the Random Assortment with the difference only concerning the formation of the two highest ranks in an assemblage, the observed discrepancy with regard to the second rank is considered to indicate a significant departure from this model. Thus, the Random Assortment model offers a better explanation for the observed pattern of species abundance than does the Composite model.

#### *Inconsistency of Geometric Series model*

Because of its deterministic nature, the Geometric Series model is applicable not only to averaged rank-abundance data but also to individual data from separate occasions. Considering the apparent closeness between the Geometric Series and the observed patterns in terms of both number and biomass for the data set A (Figs 3 and 4), an

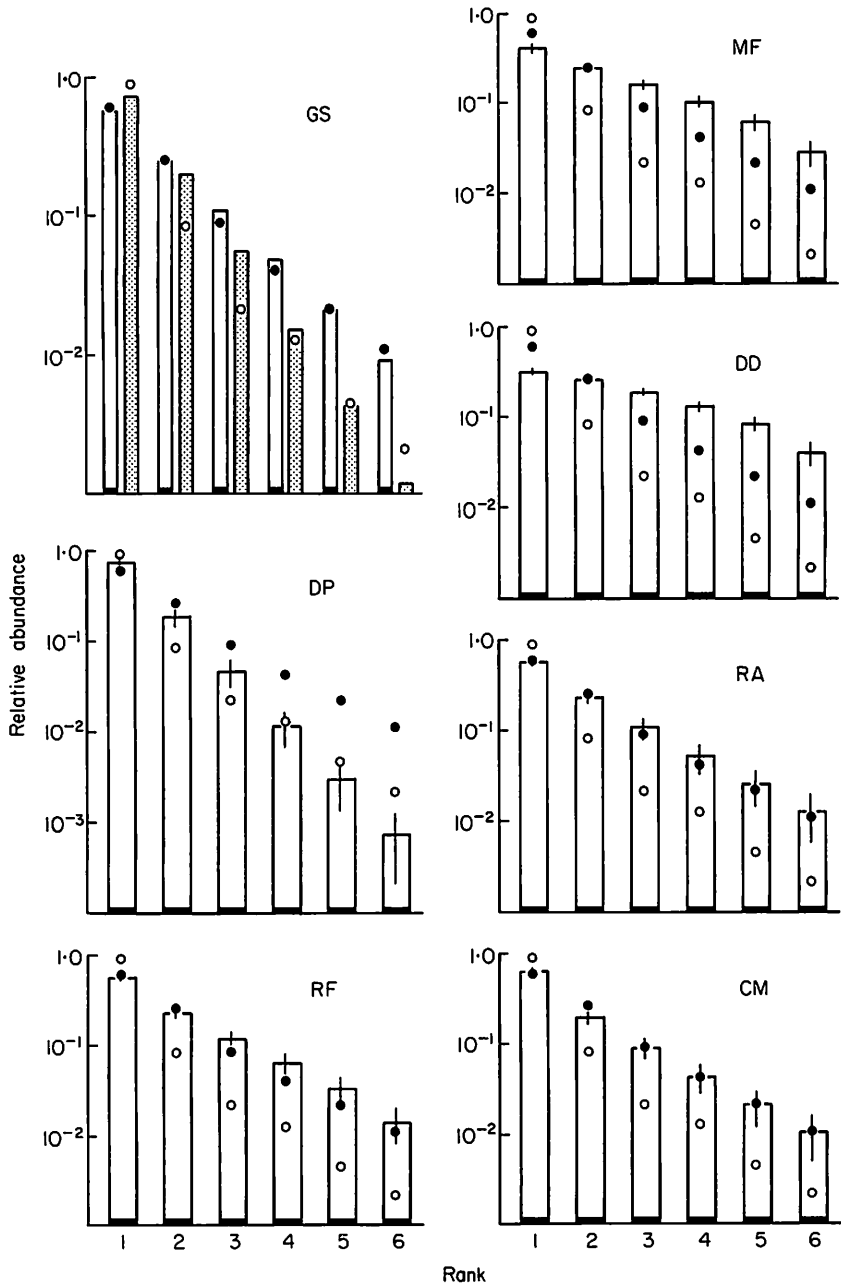


FIG. 4. As in Fig. 3, but data based on biomass rather than number of individuals.

important question to emerge is how consistent the parameter  $k$  is across the spectrum of patterns exhibited by individual data. If the Geometric Series offers a truly appropriate mechanism for abundance pattern in a community, the parameter  $k$  should demonstrate reasonable constancy in value. The results of separately fitting the model to each of the twenty-six data of the data set A (Fig. 5) show that this is not the case. For both the numerical (Fig. 5a) and the biomass (Fig. 5b) data, maximum likelihood estimates of the

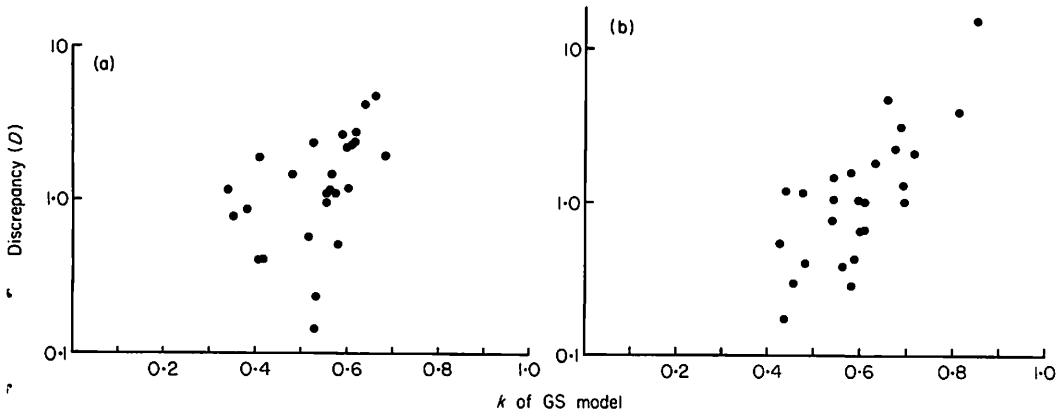


FIG. 5. Discrepancy ( $D$ ) between observation and Geometric Series model plotted against parameter  $k$  for data set A: (a) numerical data; (b) biomass data.

parameter  $k$  scattered substantially, ranging between 0.341–0.685 and 0.428–0.853 for number and biomass, respectively. Furthermore, fit between model and observation was generally poor, as indicated by relatively large values of the discrepancy  $D$ , with more than half of them exceeding 1.0. Therefore, it is unlikely that  $k$  possesses any significant meaning with respect to the species-abundance patterns in the chironomid community under study.

## DISCUSSION

### *What is being examined?*

Despite a substantial amount of effort being directed towards applying models to data on species-abundance patterns in the past (see Whittaker 1975; Frontier 1985; Gray 1987), the scientific philosophy of this endeavour has remained at best obscure. It has sometimes been argued that fitting of models (particularly statistical ones) is a useful exercise in order to uncover hitherto-unknown patterns in community ecology, even if those patterns cannot sufficiently be explained for the time being (Pielou 1975; Engen 1978). A major but often neglected problem of this approach is that, by regarding models as 'useful' community descriptors, emphasis is inadvertently placed on models rather than on real communities. This can perhaps be best illustrated with reference to the status of the log-normal model. This model has been shown to fit a variety of ecological communities (e.g. Hairston & Byers 1954; Preston 1962; Patrick 1968). However, there are a range of opinions as to the precise mechanisms leading to such a model, from largely statistical to ecological (Aitchison & Brown 1966; Bulmer 1974; May 1975; Sugihara 1980; Ugland & Gray 1982). Indeed, the Random Fraction model can be considered as a niche-apportionment analogue of the log-normal model (Pielou 1975). It is most likely that, rather than one of these being correct and all the others incorrect, all are correct to some extent at least, suggesting that the log-normal can arise from a variety of reasons. Under these circumstances a successful fit of this model to a particular data set does not prove anything. Moreover, the fact that it fits a variety of data can be interpreted to indicate the model's flexibility in assuming different forms, rather than different communities having a single underlying assembly rule common to all. Thus, patterns

revealed through model-fitting exercises would relate more to the model concerned than to the structure of real communities.

Theoretical ambiguities are a clear disadvantage to a model, if the ultimate goal of its use is to enhance understanding of the organization of communities. In this respect, niche-apportionment models are less taxed with ambiguities in their formation and appear to offer more straightforward explanations of species-abundance patterns, particularly for small communities. However, there has never been an attempt to give a logical coherence to a range of possible models of this type, leaving another class of ambiguity in the overall theoretical framework of niche apportionment. Indeed, the traditional way of classifying the two niche apportionment models, the Geometric Series and the MacArthur's Broken-Stick, as sequential breakage and simultaneous breakage model, respectively, has contributed more to the maintenance of internal disparity rather than to encouraging the search for a unifying picture.

#### *Global or community-specific pattern*

Apart from theoretical ambiguities described above, there are other, practical issues to be considered in the analyses of species-abundance patterns. One of these concerns the nature of communities to be analysed with these models. Some workers, particularly theoreticians, tend to stress a global pattern of structure across a diverse array of communities, whilst others are more inclined to seek community-specific patterns. In theory, the former approach implicitly assumes different communities as replications originating from a single hypothesis whereas the latter requires replicated observations from a single or a number of similar communities.

Sugihara (1980), following Preston's (1962) work on the canonical log-normal model, suggested that a hierarchical niche-apportionment model (in fact a variant of the Random Fraction model) could account for a wide variety of data on species patterns and termed the idea as minimum community structure. His approach was to examine taxonomically related two- and three-species assemblages first and then to extrapolate to larger assemblages. It is notable here that three-species assemblages treated in this way correspond in principle to the combination of Dominance Preemption and Dominance Decay models in the present study, which represent two outer extremes of the family of niche-apportionment models centred around the Random Fraction (Fig. 1). When extended to assemblages containing more than three species, however, theoretical discrepancies between these three models become more pronounced. Thus, a simple extrapolation of the three-species situation to the one with many species could imply the coverage of all the possibilities of niche apportionment presented here. Under these circumstances it is difficult to discern which one of the mechanisms is prevailing in the system as 'minimum community structure'. In fact, it may be perfectly reasonable to consider this as a non-structure, because very little has in reality been revealed about community organization through this approach, apart from a vague possibility that niche apportionment of some kind may be in operation. This relates in a wider context to the difficulty of seeking global patterns in species abundance, or indeed in any aspect of community ecology, though such an approach is intuitively appealing. As long as there are a variety of theoretical possibilities, some leading to similar results (cf. Random Fraction and Random Assortment), and stochastic variations in natural communities which could mask small but real differences among communities, search for a global pattern in nature is unlikely to be met with more than a cursory success.

*Community-specific pattern: to what does it refer?*

The kind of ambiguity associated with the inter-community approach is at least reduced in degree when one deals with patterns specific to different communities. On the other hand there remain other problems, one of them referring to what to expect about community-specific structure, particularly in relation to the application of niche-apportionment models. One interesting point concerns the species-orientated as against the process-orientated interpretation of niche apportionment. In the former, niches to be apportioned and ranked are assumed to be associated with the same ranking of species, i.e. the largest niche always belongs to species *a*, the second largest to species *b*, etc. Evolution is considered to have fixed the niche size of each species within a certain limit, according to a division rule specified by a particular niche-apportionment model. In contrast, the latter interpretation assumes no correspondence between niche ranking and species; species *a* can take up any rank in terms of abundance within a community. In this case what is preserved as a pattern of this community through evolution is a division rule, how niche should be apportioned among a number of species, wherein species identity is of little importance. In theory, it is of course possible to conceive of a grade of intermediate situations between these two cases. The choice between these two interpretations is likely to be influenced by the kind of community to be examined. If one deals with a relatively static community on either temporal or spatial scale, the species-orientated hypothesis may be more appropriate. In contrast, a very dynamic community with frequent appearance and disappearance of constituent species may make the process-orientated hypothesis more relevant. The latter is the view adopted in analysing the epiphytic chironomid community in the present study, as it is a highly dynamic system (Tokeshi & Townsend 1987). It is interesting to note, however, that none of the niche-apportionment models considered has been fitted successfully to the biomass data. This point is further dealt with in the next section.

*Analysis of real data: epiphytic chironomids*

Even if one intends to deal with a species-abundance pattern specific to one type of community, some practical difficulties and subtleties of analysis do not instantly dissolve, as can be seen in the present analyses of an epiphytic chironomid community. The problem of replications in testing models as has been mentioned earlier can be alleviated with experimental data involving manipulated species assemblages but, in principle, the thrust of the analysis of species-abundance patterns should always lie with natural communities. Therefore, some degree of arbitrariness and incompleteness in replications is inevitable as it is always necessary to choose a more or less arbitrary scale of time or space for those replications. In the chironomid data under study, the data set B apparently constituted a collection of inappropriate replications which can be interpreted to represent, in effect, a single replication.

Another problem concerns the use of number or biomass to express species abundance. For some groups of organisms this distinction may not be of much importance but for the majority it cannot easily be ignored. Ambiguity in this respect is exacerbated by the fact that there have been few attempts to use both the number of individuals and biomass from the same community in analysing species-abundance patterns. Intuitively, if niche is equated with resource in the formulation of niche-apportionment models, species abundance as expressed by biomass appears to make better sense, as it will be more closely related to the concept of resource utilization. The often-mentioned dimensionality of niche (Hutchinson 1957; Whittaker 1977; Pianka 1981; Sugihara 1980) can conceptually

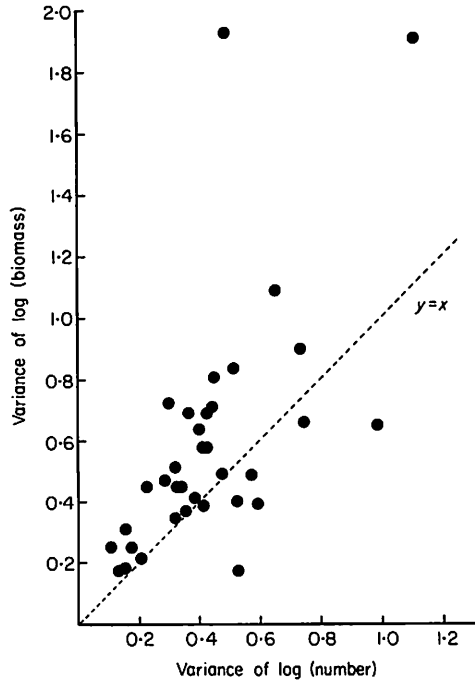


FIG. 6. Variance of log (biomass) plotted against variance of log (number) for the epiphytic chironomid data. Dashed line shows  $y=x$ .

be interchanged with resource dimensionality (Schoener 1974, 1986). On the other hand, it seems of doubtful value to incorporate the multi-dimensionality argument into the niche-apportionment models, as long as the total niche or resource pool (multi- or single-dimensioned) of a community is crudely likened to a mass or stick to be divided, particularly in view of our very limited knowledge on the precise relationship between different niche dimensions in assemblages containing more than three species.

Recently, Harvey & Godfray (1987) used an allometric argument to suggest that species abundance as expressed by biomass would have a more equitable pattern than that expressed by number of individuals. Sugihara (1989) put forward a counter argument, suggesting that equitability or variance of species abundance would be roughly the same for numerical and biomass data. If the latter argument holds, analysis can equally be carried out using measurements based on either number or biomass. Variance of the logarithms of biomass plotted against that of number for the chironomid data (Fig. 6) reveals an interesting picture. Because the points do not systematically fall below the 45° line (i.e.  $\text{var}[\log B] \ll \text{var}[\log M]$ ), Harvey & Godfray's argument is rejected. On the other hand, Sugihara's argument can hardly be supported, because a significantly larger number of points (binomial test,  $P < 0.001$ ) lie above the line: species abundance in terms of biomass is less equitable than that in terms of number. Thus, there seems to be no convenient recipe to rely upon with respect to the expression of species abundance in this and perhaps many other communities, apart from an intuitive plausibility that biomass reflects niche or resource use more closely than does number.

The above discussion notwithstanding, it is interesting to observe that the Random Assortment model successfully fitted both the numerical and biomass data. This means



that the discrepancy between these two data, though real as is shown in Fig. 6, can still be accommodated within the normal variation of Random Assortment. Note that as far as the logic of RA model goes, it may apply to both numerical and biomass data at the same time without necessarily assuming a particular relationship between number and biomass in a community; in some communities including the present, epiphytic chironomids numbers and biomass could fluctuate through time almost independently of each other. The fact that none of the niche-apportionment models achieved a successful fit to the biomass data (which is thought to be more closely related to the niche concept as mentioned above) lends support to the view that the chironomid community is not structured by the process of niche apportionment as envisaged by the models presented. Rather, the satisfactory fit of the RA model points to a dynamic, unpredictable community, at least during spring and early summer when resource utilization is at its highest level in this community (Tokeshi 1986b). It remains to be seen whether this model has wider applicability in other (dynamic) communities; more rigorous data collection and analysis may prove fruitful in that respect.

### ACKNOWLEDGMENTS

I thank Dave Jewson, Ian Winfield, Brian Wood, Brian Rippey and all the other members of the Freshwater Laboratory at Traad Point, University of Ulster, for various forms of logistic support during the course of this work, Sean Nee and Robert May of the University of Oxford and John Gray of the University of Oslo for kindly reviewing the manuscript.

### REFERENCES

- Aitchison, J. & Brown, J. A. C. (1966). *The Lognormal Distribution*. Cambridge University Press, Cambridge.
- Bulmer, M. G. (1974). On fitting the Poisson lognormal distribution to species-abundance data. *Biometrics*, **30**, 101–110.
- De Vita, J. (1979). Niche separation and the Broken Stick Model. *American Naturalist*, **114**, 171–178.
- Engen, S. (1978). *Stochastic Abundance Models with Emphasis on Biological Communities and Species Diversity*. Chapman & Hall, London.
- Fisher, R. A., Corbet, A. S. & Williams, C. B. (1943). The relation between the number of species and the number of individuals in a random sample from an animal population. *Journal of Animal Ecology*, **12**, 42–58.
- Frontier, S. (1985). Diversity and structure in aquatic ecosystems. *Oceanography and Marine Biology: An Annual Review*, **23** (Ed. by M. Barnes), pp. 253–312. Aberdeen University Press, Aberdeen.
- Gray, J. S. (1987). Species-abundance patterns. *Organization of Communities: Past and Present* (Ed. by J. H. R. Gee & P. S. Giller), pp. 53–67. Blackwell Scientific Publications, Oxford.
- Hairston, N. G. & Byers, G. W. (1954). The soil arthropods of a field in southern Michigan: a study in community ecology. *Contributions from the Laboratory of Vertebrate Biology, University of Michigan*, **64**, 1–37.
- Harvey, P. H. & Godfray, H. C. J. (1987). How species divide resources. *American Naturalist*, **129**, 318–320.
- Hughes, R. (1984). A model of the structure and dynamics of benthic marine invertebrate communities. *Marine Ecology Progress Series*, **15**, 1–11.
- Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposium on Quantitative Biology*, **22**, 415–427.
- Kempton, R. A. & Taylor, L. R. (1974). Log-series and log-normal parameters as diversity discriminants for the Lepidoptera. *Journal of Animal Ecology*, **43**, 381–399.
- MacArthur, R. H. (1957). On the relative abundance of bird species. *Proceedings of the National Academy of Science, USA*, **43**, 293–295.
- MacArthur, R. H. (1960). On the relative abundance of species. *American Naturalist*, **94**, 25–36.
- McNaughton, S. J. & Wolf, L. L. (1970). Dominance and the niche in ecological systems. *Science*, **167**, 131–136.
- May, R. M. (1975). Patterns of species abundance and diversity. *Ecology and Evolution of Communities* (Ed. by M. L. Cody & J. M. Diamond), pp. 81–120. Belknap/Harvard University Press, Cambridge, Mass.
- Motomura, I. (1932). On the statistical treatment of communities. *Zoological Magazine, Tokyo*, **44**, 379–383 (In Japanese).

- Patrick, R. (1968). The structure of diatom communities in similar ecological conditions. *American Naturalist*, **102**, 173–183.
- Pianka, E. R. (1981). Competition and niche theory. *Theoretical Ecology* (Ed. by R. M. May), pp. 167–196. Blackwell Scientific Publications, Oxford.
- Pielou, E. C. (1975). *Ecological Diversity*. Wiley-Interscience, New York.
- Preston, F. W. (1948). The commonness and rarity of species. *Ecology*, **29**, 254–283.
- Preston, F. W. (1962). The canonical distribution of commonness and rarity. I and II. *Ecology*, **43**, 185–215, 410–432.
- Schoener, T. W. (1974). Resource partitioning in ecological communities. *Science*, **185**, 27–39.
- Schoener, T. W. (1986). Resource partitioning. *Community Ecology: Pattern and Process* (Ed. by J. Kikkawa & D. J. Anderson), pp. 91–126. Blackwell Scientific Publications, Oxford.
- Sugihara, G. (1980). Minimal community structure: an explanation of species abundance patterns. *American Naturalist*, **116**, 770–787.
- Sugihara, G. (1989). How do species divide resources? *American Naturalist*, **133**, 458–463.
- Taylor, L. R., Kempton, R. A. & Woiwood, I. P. (1976). Diversity statistics and the log-series model. *Journal of Animal Ecology*, **45**, 255–272.
- Tokeshi, M. (1985). Life-cycle and production of the burrowing mayfly, *Ephemera danica*: a new method for estimating degree-days required for growth. *Journal of Animal Ecology*, **54**, 919–930.
- Tokeshi, M. (1986a). Population dynamics, life histories and species richness in an epiphytic chironomid community. *Freshwater Biology*, **16**, 431–442.
- Tokeshi, M. (1986b). Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. *Journal of Animal Ecology*, **55**, 491–506.
- Tokeshi, M. & Townsend, C. R. (1987). Random patch formation and weak competition: coexistence in an epiphytic chironomid community. *Journal of Animal Ecology*, **56**, 833–845.
- Ugland, K. I. & Gray, J. S. (1982). Lognormal distributions and the concept of community equilibrium. *Oikos*, **39**, 171–178.
- Whittaker, R. H. (1972). Evolution and measurement of species diversity. *Taxon*, **21**, 213–251.
- Whittaker, R. H. (1975). *Communities and Ecosystems*. 2nd edn. Macmillan, New York.
- Whittaker, R. H. (1977). Evolution of species diversity in land communities. *Evolutionary Biology*, **10**, 1–66.

(Received 27 September 1989)