

Species Abundance Patterns and Community Structure

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I. SUMMARY

Despite the fact that a substantial research effort has been directed at the analysis of species abundance patterns over the years, there are many important issues which are not sufficiently explored and understood. This review examines the conceptual and methodological frameworks of analysis in species abundance patterns, with particular emphasis on interpreting patterns in the context of community structure and organization.

Historically, this discipline underwent a largely monotonous pattern of development (Section III) in that successive researchers proposed different models which were often claimed to be superior to those previously proposed, followed by seemingly piecemeal analyses of empirical data with reference to a particular model. This has resulted in a conspicuous lack of broad perspective in the study of species abundance patterns, despite a number of reviews produced. In the first place, therefore, it is important to clarify the conceptual basis of analysing species abundance patterns, including the definition of community and sample to which different models inevitably refer (Section IV). Basic characteristics of species abundance models proposed to date are briefly reviewed and recommendations for standardizing the presentation of rank-abundance graphs are given.

In the context of unravelling community structure, the concept of niche is highly relevant in the analysis of species abundance patterns (Section V). Thus particular attention is given to the development of niche-oriented models with a consideration of the relationship between resource and species abundance. Furthermore, with respect to the question of how total energy or resource is divided among species in a community, the current debated issue of density-body size allometry is reviewed.

Interpretation of models and patterns is a major problem in this discipline (Section VI). It is recognized that models, particularly niche-oriented ones, are useful in suggesting possibilities underlying community organization. Thus they should be regarded as an aid for interpreting patterns rather than as a precise and rigid description of mechanisms involved. Consideration is given to some important dichotomies including global versus community-specific patterns, contemporary versus evolutionary processes, species- versus process-oriented interpretation and equilibrium versus non-equilibrium communities.

Apart from problems associated with interpretation, there are practical problems of testing models (Section VII). Despite empirical studies in the

past, this is again a neglected area, and particular difficulties arise with stochastic species abundance models. As a way forward, a simulation method of testing stochastic-type models is introduced and the importance of making replicated observations is emphasized.

Section VIII deals with topics which are closely related to the analysis of species abundance patterns, namely diversity indices, species–area relationships and application to environmental assessment. Section IX identifies aspects to be considered in future investigations and emphasizes the importance of spatial/temporal variability and of integrating the analysis of species abundance patterns and other analyses of community structure, whether observational, experimental or analytical, in order to achieve a better understanding of ecological communities.

II. INTRODUCTION

A. Objectives of Analysing Species Abundance Patterns

The recognition and interpretation of patterns lies at the heart of an emerging scientific discipline such as community ecology. This twin aspect is often difficult to achieve, especially when there is a lack of general conceptual and methodological frames of reference within the science in question. Concept without methodology runs the risk of spurious analysis, while methodology without concept may lead to irrelevant analysis. To constantly assess the conceptual and methodological integrity of a field provides an important basis on which to develop a sound process of pattern recognition and interpretation. Analyses of species abundance patterns in community ecology seem to have suffered, to various degrees, from this broad problem. It is in this context that issues relating to species abundance patterns are reviewed here. Mathematical exposition of models, which has repeatedly been carried out in previous reviews, is not intended here; reference should be made to May (1975) and Pielou (1975) in particular.

Measuring the abundance of a species is a starting point of modern population/community ecology (see Andrewartha and Birch, 1954; Begon *et al.*, 1986). When one investigates any animal or plant community it is ubiquitously observed that some species are common and others are rare; species can be arranged on a spectrum of abundance from the commonest to the rarest. This immediately raises the question: Is there any way of describing abundance relationships of different species that may help us understand how a community is organized? Faced with this challenge, ecologists have traditionally adopted one of two approaches—these may conveniently be described as the *mechanistic* and the *static* approaches.

In the mechanistic approach the relative abundance of species is used as a basic measure with which many of the phenomena affecting communities

such as predation, competition and disturbance are analysed; indeed, investigators often employ the general term "community structure" to mean no more, or less, than the relative abundance of species in a community, when purporting to elucidate the influences of abiotic and biotic factors that may be operating in a given community. Thus this approach stresses mechanistic aspects of species abundance, implicitly assuming that a species abundance pattern represents a kind of dynamic equilibrium state which is susceptible to variation on spatio-temporal scales and that this variability is mostly observable under experimental conditions. By contrast, the static approach focuses attention on the pattern of species abundance *per se*, rather than on factors which may influence it, in an attempt to seek suitable methods of description which, hopefully, provide some understanding of underlying mechanisms. In other words, the static approach concentrates on describing and interpreting a "snapshot" of species abundance patterns and unravelling overall processes leading to such a snapshot, while the mechanistic approach emphasizes the identification of currently-operating factors and mechanisms that produce variation in snapshots.

Considered in this way the two approaches are not in conflict but complementary; contemporary processes are the focus of analysis in the mechanistic approach to species abundance patterns, whilst broader, evolutionary processes are often implicated in the static approach. On the other hand, these distinctions can easily be blurred and there is a substantial conceptual overlap, which should allow exchange of ideas between the two approaches. In reality, however, the mechanistic and static approaches to species abundance patterns have so far taken independent courses of development, with very little exchange of ideas. Indeed there are very few studies which have analysed a single community using both the mechanistic and static approaches. Whilst the mechanistic approach has flourished with the popularity of short-term experimental investigations in the past few decades, the static approach has experienced a somewhat stalled development and has been relegated to a comparative obscurity. This is partly due to the stereotype of the analytical framework of the latter approach that failed to inspire field ecologists, and to the lack of sufficient appreciation of many issues involved. This is a rather unfortunate state of affairs, since species abundance patterns will undoubtedly continue to represent one of the most fundamental aspects of ecological communities, and yet ecologists will remain incapable of deriving useful information and giving plausible explanations, particularly in the context of possible linkage between contemporary and evolutionary processes.

Whilst it may be argued that species abundance patterns have received less attention than they deserve, another measure of ecological communities, namely diversity, which is based on the same information as species abundance patterns, has been widely used, in spite of the methodological

difficulties and ambiguities associated with it. The irony is that a single value of a diversity index expresses less information than does a full species abundance pattern with respect to a given community. This imbalance of attention given to species abundance patterns and its derivative diversity is largely attributable to the conceptual appeal of the latter rather than to any scientific rigour or superiority attached to it. Thus, if diversity is accepted as a useful measure of communities, so should species abundance patterns be; there are no objective scientific grounds for regarding the latter with disfavour in comparison with the former. Indeed the latter may be preferable if a detailed analysis of a community is intended. It then follows that description of species abundance patterns represents as worthwhile an endeavour as does the description of diversity.

Description of patterns is more meaningful if it is accompanied by a mechanistic understanding of the processes involved. Whilst this is not always straightforward, or indeed possible (see Section VI), it is at least worthwhile to consider the reasons and nature of the difficulties encountered in such cases; this may lead to other possibilities and/or better understanding. In this respect it is important to note that any described pattern is worth interpreting, irrespective of whether or not the pattern is related to some tangible processes within a community (Tokeshi, 1990a).

One trend that characterized the past analyses of species abundance patterns is the emphasis placed on theoretical models and their mathematical properties. This by itself is not an undesirable situation; on the contrary, it is absolutely necessary as a basis of understanding. However, what seems to have affected the development of this field is the corresponding lack of emphasis on the practicality of applying these models to real data and subsequent interpretation. In other words, recognition and interpretation of species abundance patterns have not adequately been extended beyond models to real communities. Therefore, this remains as an area of major challenge in this discipline—a point that is emphasized throughout this chapter.

Analyses of species abundance patterns need to be considered as forming an integral part of community ecology, rather than as representing a peculiar digression (mostly in the past) that is better ignored. In this respect it should be noted that the fact that this field has not had much impact within community ecology does not necessarily imply an inherent unimportance and inability to contribute to the overall development of community ecology. Whilst describing and interpreting species abundance patterns alone will not lead to an unambiguous understanding of ecological communities, it is equally certain that no other analytical approach can achieve the goal separately; a combination of different methods and approaches is the surest way available to us to reach a higher level of understanding.

III. HISTORICAL PERSPECTIVES

One way to grasp the general trend of research on species abundance patterns is to see how the subject has been treated in primary papers, reviews and general ecology textbooks. Despite relative unpopularity among field ecologists, models of species abundance patterns have frequently been reviewed in the past two decades. This section is intended as a concise sketch of the course of development in this discipline, not as an exhaustive survey of the literature.

A. Original Works

The earliest attempt to suggest the relationships of relative abundances in a community was by Motomura (1932), who examined several data sets on benthic faunas of lakes and proposed the geometric-series model as an empirical relationship. His primary interest was to consider as simple a method as possible to describe ecological communities with particular reference to the complexity of species composition. Originally this model was simply treated as a convenient descriptor of ecological communities rather than as representing biological processes; the aspect of sequential niche apportionment was later stressed by other investigators. Unfortunately the original paper was written in language inaccessible to Western scientists and his intention seems to have been slightly misunderstood.

Fisher *et al.* (1943) suggested the log-series model as an appropriate description of frequency distributions of the number of species against the logarithmic number of individuals per species. The model has been fitted to a variety of species-rich assemblages, particularly insects (Williams, 1944, 1964), and its properties as applied to real data have been thoroughly investigated by Kempton and Taylor (1974) and Taylor *et al.* (1976). Furthermore, Taylor (1978) and Kempton and Taylor (1974, 1976) analysed the parameter α of the log series which Williams (in Part II of Fisher *et al.*, 1943; Williams, 1944) proposed as an index of diversity.

Adopting a somewhat similar approach to Fisher *et al.* (1943), Preston (1948) considered the problem of commonness and rarity using a range of insect and bird data, and suggested the log-normal model of species abundances, whereby what Preston later called the "canonical" hypothesis (Preston, 1962) came to receive particular attention. May (1975) investigated in detail the mathematical properties of this model and considered that the pattern was essentially a statistical consequence of large numbers (the central limit theorem). Similarly, Ugland and Gray (1982) argued that the characteristics relating to the canonical log-normal are based on the mathematical properties of the model. In contrast, Sugihara (1980) suggested a possible biological foundation of this model in the form of a "hierarchical niche break-age" hypothesis. This point is examined further in later sections.

The negative binomial distribution has frequently been used for analysing spatial distributions of populations (e.g. Bliss and Fisher, 1953; Bliss and Owen, 1958; Lyons, 1964), but has rarely been applied to species abundance patterns as a descriptive model (e.g. Brian, 1953; Kempton, 1979). However, since the log series is a limiting form of the negative binomial (Fisher *et al.*, 1943; Anscombe, 1950), the statistical properties of the latter (particularly as a zero-truncated form) were extensively discussed by Pielou (1975) and Engen (1978) in the context of species abundance patterns.

MacArthur (1957) was the first to question the practice of fitting statistical models of uncertain biological meaning to real data and suggested as an alternative the construction of models based on simple biological hypotheses and their comparison with data. He proposed three such hypotheses relating to equilibrium/near-equilibrium populations, among which what he called "hypothesis I" came to be widely known as the "broken-stick model"; Cohen (1968) presented an alternative explanation for this model. The other two hypotheses, the overlapping-niche model and the particulate-niche model, which MacArthur (1957) himself considered unsatisfactory, have subsequently received scant attention and no attempt has been made to test them with real data. In fact, theoretical interest apart (e.g. Webb, 1974), the broken-stick model itself had not witnessed a rigorous testing before Tokeshi (1990a) discussed in detail the problems associated with testing stochastic species abundance models in general and adopted a new approach (see Section VII.A).

Caswell (1976) introduced a rather unique approach to the study of species abundance patterns. He used a neutral model of stochastic community development which was originally applied in population genetics (Karlin and MacGregor, 1967, 1972; Ewens, 1972; Watterson, 1974) to generate species abundance patterns supposed to be free from biotic interactions. Comparison between the predictions of neutral model and observed patterns revealed that real communities are in general less diverse, in terms of both species richness and equitability, than would be expected under neutral conditions.

Frontier (1985) introduced a family of models termed the "Zipf-Mandelbrot model", which had previously been used in linguistics and socio-economic contexts and modified by Mandelbrot through a mathematical analysis of information management (Zipf, 1949, 1965; Mandelbrot, 1977, 1982). Detailed exposition of the model as applied to ecological data is given in Frontier (1985), but the elaborate biological analogies regarding successional processes have yet to be justified in the light of real ecological phenomena. The model may indeed be considered no more biological than the log-series or the log-normal models.

Hughes (1984) criticized the log-series and the log-normal models as inappropriate descriptors of species abundance patterns, and instead proposed

the dynamics model that incorporated ecological processes thought to be important in many marine benthic assemblages. Subsequently he claimed that the model agreed well with the majority of 222 data sets of a wide range of communities on the basis of visual inspection of the shapes of species abundance patterns (Hughes, 1986).

Tokeshi (1990a) shared the doubt about the application of statistically orientated models (MacArthur, 1957; Hughes, 1984; Lamshead and Platt, 1985) and concentrated on giving logical coherence to niche-orientated models, particularly in consideration of relatively small communities of closely related species. This work was unusual in the tradition of research on species abundance patterns, in the sense that the problems of application and interpretation were given prominence. In addition, seven models including some new ones (the geometric series, dominance pre-emption, random fraction, MacArthur fraction, dominance decay, composite and random fraction) were compared with real data using a new analytical technique.

B. Reviews and Ecology Texts

Amongst reviews, May (1975) carried out a particularly thorough investigation of the mathematical properties of four models known to that date, i.e. the geometric series, the log series, the log-normal and the broken stick. Pielou's (1975) review is an equally lucid exposition of the mathematics of these four models plus the (truncated) negative binomial. The latter review also drew attention to some difficulties of testing these models, but Pielou's remarks did not seem to have found their way through to the minds of practising field ecologists. These two publications represented a significant advancement of knowledge, but might have created an unfortunate image of this discipline—interesting for theoretical research but unappealing to field ecologists. Engen's (1978) treatment of stochastic abundance models including those mentioned above plus Zipf's model was also mathematical in nature and may have served to reinforce this image. In contrast to these primary reviews of the 1970s that have contributed substantially to the furtherance of theoretical understanding, three reviews published in the 1980s (Kikkawa, 1986; Gray, 1987; Magurran, 1988) assumed more of a didactic nature with emphasis on the presentation of previous works rather than on original synthesis. In this respect, Frontier's (1985) review is unusual in strongly advocating one model (the Zipf–Mandelbrot model) which has rarely been used in the biological context.

As a general ecology text, Ricklefs (1973) gave a lucid account of the log-normal model and MacArthur's three models (especially the broken stick model) in the ecological context. Similarly, Colinvaux (1973) gave a most detailed account of the research development with respect to the broken-stick model, while Whittaker (1975) described the broken-stick, the geo-

metric-series and the log-normal models with reference to the niche concept. Despite these attempts, the general lack of overview and the fact that the analysis of species abundance patterns has not fully been explored with real data seem to be reflected in the restricted treatment of this subject in general ecology texts. Indeed, neither Krebs (1972), Ricklefs (1973), Colinvaux (1973), Whittaker (1975), or Begon *et al.* (1986) treated *all* the four earlier models (geometric series, log series, log-normal and broken stick), not to mention other models, in the context of applying them to real communities. It is notable that (as of early 1990s) the latest and currently most popular text by Begon *et al.* (first edition, 1986; second edition, 1990) does no more than present a very brief explanation of this subject with a single graph showing theoretical curves of the geometric-series, the log-normal and the broken-stick models. This may perhaps accurately mirror the current level of interest (and indeed understanding) on the part of practising ecologists, which is also reflected in the way the subject is treated in the three recent reviews mentioned earlier. It will be unfortunate, however, if this is to be construed as a sign of verified “uselessness” of research on species abundance patterns; in the present circumstances the lack of imagination and rigour in the past/present analyses should firstly be guarded against. In this respect there is no justification for limiting our attention to the log-series, the log-normal, the geometric-series and the broken-stick models. Furthermore, whilst it is unreasonable to expect too much from a single analytical approach to community ecology, it is equally unreasonable to reject one particular approach on the basis of an impression which might have been nurtured through a somewhat biased research tradition.

IV. THE BASIS OF SPECIES ABUNDANCE MODELS

A. Community Definition and Scales

Any analysis in community ecology is ultimately dependent on the meaning attached to “community”. Indeed, how it is perceived by different investigators under different circumstances may to some extent explain discrepancies in interpretation and attitudes towards different models or analyses. The generally accepted definition of a community as “an assemblage of populations of animal and plant species living together within an area” is sufficiently vague to allow a multitude of interpretations when applied to different situations. Whilst this may lead to a healthy proliferation of approaches, it would always be necessary to recognize differences in premises which bear upon final analytical results. Here, it is worth giving some attention to three aspects that demarcate an ecological community: taxonomic, spatial and temporal boundaries.

Despite the potentialities of dealing with taxonomically distant species as members of a single community (e.g. herbivorous insects and mammals in a grassland, fish and zoo/phyto-plankton in lakes, and trees and mosses in a forest)—an approach which is positively desirable in some areas of community—studies of species abundance patterns in general have adopted a narrower view of the community, i.e. an assemblage of closely related species or a trophic guild (e.g. foliage-gleaning birds, stream diatoms, Lepidoptera attracted to light traps, herbaceous plants in a chalk grassland, benthic invertebrates, etc.), as in many studies on competitive relations in a community. This is a reasonable approach, since life-history characteristics as well as resource bases are often very different among taxonomically distant taxa, making it less meaningful to discuss relationships of relative abundances among them. At the same time it is very difficult to take samples of taxonomically distant organisms with equal efficiency on the same spatial scale, rendering their abundance estimates less comparable. There is also a more practical consideration of the nature of taxonomic expertise generally available; species identification can most reliably be achieved within a single taxonomic group with which one is familiar. Indeed, different levels of uncertainty in species identification among different taxa may introduce further complication in the analysis if taxa are to be amalgamated as a single community.

In addition to the taxonomic aspect, the spatial and temporal extent of communities poses a serious practical problem which tends to defy an attempt to reach an objective solution. Spatial and temporal boundaries of a community are often indistinct and need to be determined arbitrarily according to the objective of research and the practicality of sampling. In some cases such as terrestrial fauna/flora on oceanic islands and parasite communities of mammalian hosts there is little difficulty in recognizing an apparent spatial boundary; this, however, applies to one level of spatial scale only, and every community exists on a hierarchy of spatial scales. Similarly, the temporal extent of a community can variously be defined, especially in relation to the patterns and lengths of life cycles of the species involved. In particular, communities which undergo rapid changes in relative abundances of constituent species will require a careful consideration of the temporal aspects. Explicit recognition of spatial and temporal variation of a community is something which is yet to be achieved in the analyses of species abundance patterns. The current debate concerning the importance of spatial/temporal scales of investigation in the understanding of patterns and processes in ecological communities (e.g. Dayton and Tegner, 1984; Gee and Giller, 1987; Rahel, 1990) is highly relevant to the analysis of species abundance patterns in general where scale effects have not traditionally been taken into account.

Whilst the study of species abundance patterns naturally lies in the domain

of community ecology, it is worth noting that the data sets to which one of the earliest models of species abundance, the log-series model, was applied were referred to as "collections" rather than "communities" (Fisher *et al.*, 1943). This judicious choice of the term presumably reflects the authors' recognition that samples such as those gathered by light traps cannot usefully be considered as belonging to a community in the normal sense of the word, notwithstanding the fact that "community" is itself a fairly elusive notion to start with. It is also notable that the subsequent development of research on the log-series model has almost exclusively dealt with "collection" type data that have no effective spatial/temporal definition (see Kempton and Taylor, 1974, 1976; Taylor *et al.*, 1976). Indeed it is worth stressing that the kinds of data to be handled by models such as the log series, the log normal and the truncated negative binomial tend to have fairly vague spatial and temporal boundaries, making it very difficult to define a community. In the case of the log-normal model it is well known that the left-hand tail of a log-normal species frequency distribution is gradually revealed as sampling is conducted on a larger spatial and/or temporal scale, thus encompassing more heterogeneous assemblages of species. Therefore, in theory, the log-normal model can be interpreted as an ideal representation of a boundless assemblage of species, which can hardly be called a "community". This does not automatically negate the possible application of models such as the log-series and the log-normal models to communities which are spatially/temporally better defined, but their background as such should always be taken into account, especially if comparison is to be made with other models and consideration is given to the relevance of models in unravelling "community" organization.

B. What Does a "Sample" Represent?

The arbitrary nature of community definition is further confounded by the need to rely on samples which represent a small portion of a presumed "community". In the vast majority of cases it is impractical/impossible to do a census of all the individuals in a given area and, therefore, some kind of sampling is called for. If inference is to be drawn from samples, it is important to know the accuracy with which samples reflect patterns pertaining to the community; however, accuracy cannot be assessed objectively unless we know thoroughly the composition of the parent community, in which case there would be no need to take samples in the first place. This logical dilemma is particularly acute in the analyses of species patterns where relative abundance, which is highly susceptible to the vagaries of sampling, is itself the focus of attention.

Faced with the uncertainty of what a sample represents, an alternative approach that has been frequently adopted, often unconsciously, is to treat

the sample as if it were an entire community in its own right. In other words sampling is not recognized as being different from censusing, irrespective of the background definition of a community under study, thus creating a false impression that a sample constitutes a self-contained entity. This would automatically eliminate the need to consider the problem of stochasticity and variations due to sampling, and researchers can feel content with unrepliated data. Models can be applied directly to such data (but, see later sections) and results discussed in terms of community structure. In fact, the majority of past studies fall into this mould, largely accounting for the conspicuous lack of perspectives on spatio-temporal scales and variability in species abundance patterns.

When it is acknowledged that censusing all the individuals in a community is not a practical proposition and that sampling cannot be equated with censusing, random sampling is considered to offer the best prospect of accurately revealing community patterns. Here, it is important to note that in the context of analysing species abundance patterns "randomness" in sampling is meaningful only if it refers to individuals of different species, i.e. each individual has the same probability of being sampled. Under normal circumstances, however, random sampling simply refers to the spatial arrangement of sampling units such as quadrats and traps, which does not necessarily lead to random sampling of individuals. In this respect, while it is impossible to guarantee complete randomness in sampling individuals in any situation, it is at least worthwhile to avoid sampling procedures that are prone to a strong bias. For example, attraction to a certain type of light trap can vary among different species of moths to such an extent that relative abundances represented in those collections may not reflect the "real" relative abundances in nature. The choice of sampling methods and procedures obviously requires a case-by-case consideration, for which reference should be made to the statistical and methodological literature (e.g. Cochran, 1967; Elliott, 1977; Southwood, 1978; Snedecor and Cochran, 1980; Sokal and Rohlf, 1981; Downing and Rigler, 1984; Holme and McIntyre, 1984; Kershaw and Looney, 1985; Moore and Chapman, 1985).

Even if sampling biases are eliminated, random sampling does not necessarily guarantee the accurate representation of the relative abundances of species. The very nature of random sampling implies that species can be over- or under-represented purely by chance, thus giving a false impression of the community composition. Rare species are particularly susceptible to under-representation and may be altogether missing in a sample. This problem is more acute when one is trying to estimate the diversity indices including species richness (i.e. the total number of species) in a community, while species abundance patterns may not be so strongly influenced. Nevertheless, this is an aspect which deserves attention, since it bears upon the stochastic variation in data.

Preston (1948) was the first to describe stochastic variation in relative abundances due to random sampling. He contrasted *random* sampling with *perfect* sampling where a species is represented by the number exactly in proportion to its abundance in the whole sampling universe. Perfect sampling in this sense can only be achieved with intention; without prior knowledge of relative abundances in the sampling universe, such intention cannot rationally be formed. Thus relative abundances shown by all but perfect sampling should always be considered as being somewhat different from true values pertaining to a given community.

An aspect which is closely linked to random sampling in species abundance studies is the number of samples (sampling units) to be taken. The same problem applies to the estimation of population density, for instance; a single sample (e.g. a quadrat) cannot give a reliable value and it is necessary to take a number of replications to enable statistically meaningful estimation. Whilst this is well recognized when density is dealt with, very few studies on species abundance patterns have paid attention to this aspect. Indeed, the majority of studies unsuspectingly rely on values of a single sample or of lumped samples such that no consideration of sample replications occurs. In terms of describing patterns, such "single-sample observation" is scientifically unsound and misses important information. This problem largely arises from insufficient thought being given to what a sample represents; the total sampling universe (i.e. community) can only roughly and inaccurately be represented by a sample.

C. Model Characteristics

Different models have been developed to suit different circumstances and, therefore, it is important to have a broad view of models in comparative terms. One way to put models into perspective is to examine models according to different schemes of classification. Whilst any classification entails to some extent ambiguous boundaries and subjective judgement, it is nevertheless helpful to categorize models on common grounds.

1. *The Nature of Models—Statistical or Biological*

Models of species abundance patterns are either statistically oriented or biologically oriented in origin. Biologically oriented models can be further divided into niche-oriented models and non-niche models. These distinctions, however, are often blurred because later workers attempted to attach different meanings to original propositions and some models are indeed intermediates between statistical and biological models. For example, Sugihara (1980) suggested that a biological process can account for the canonical log-normal model which had previously been regarded basically as a

Table 1
Models of species abundance patterns

Type of model	Model	Reference
Statistically oriented	Log series	Fisher <i>et al.</i> (1943)
	Log-normal	Preston (1948, 1962)
	Negative binomial	Anscombe (1950), Bliss and Fisher (1953)
	Zipf-Mandelbrot	Zipf (1949, 1965), Mandelbrot (1977, 1982)
Niche oriented	Geometric series	Motomura (1932)
	Particulate niche	MacArthur (1957)
	Overlapping niche	MacArthur (1957)
	Broken stick	MacArthur (1957)
	MacArthur fraction	Tokeshi (1990a)
	Dominance pre-emption	Tokeshi (1990a)
	Random fraction	Tokeshi (1990a)
	Sugihara's sequential breakage	Sugihara (1980)
	Dominance decay	Tokeshi (1990a)
	Random assortment	Tokeshi (1990a)
Composite	Tokeshi (1990a)	
Other	Biological	Dynamic model
	Non-biological	Neutral model
		Hughes (1984, 1986) Caswell (1976)

statistical model (Preston, 1962; May, 1975). Similarly, the earliest niche-oriented model (the geometric series) was proposed as more of a statistical model than a biological one (Motomura, 1932). Notwithstanding these complications, Table 1 classifies models proposed to date as statistically oriented, niche-oriented or other biologically oriented. Statistically oriented models generally deal with communities which have vague spatial/temporal boundaries and contain relatively large number of species, while niche-orientated models are more relevant to small communities of related species sharing the same kind of resources. At present it is probably better to treat Sugihara's sequential niche division model separately from the (statistically oriented) canonical log-normal model.

2. *Sequential versus Simultaneous Niche Breakage Models*

Before Tokeshi (1990a) introduced a number of niche-oriented models, the geometric-series model and MacArthur's broken-stick model were often referred to as the "simultaneous breakage model" and the "sequential breakage model", respectively (e.g. Pielou, 1975). This distinction now seems unnecessary as all the niche-apportionment models, including the broken-

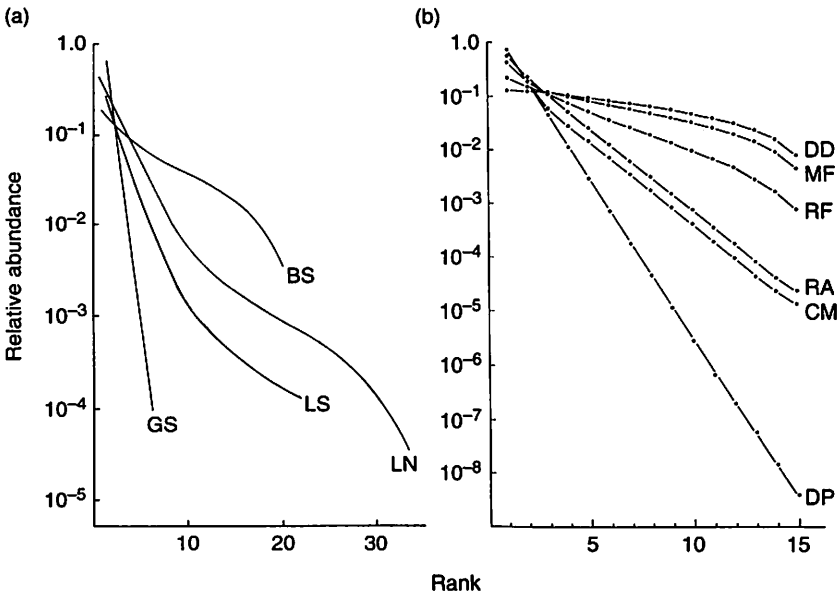


Fig. 1. Rank–abundance patterns of various models. (a) GS, Geometric series; LS, log series; LN, log-normal; BS, broken stick. (b) DP, Dominance pre-emption; CM, composite; RA, random assortment; RF, random fraction; MF, MacArthur fraction; DD, dominance decay. (After Tokeshi (1990a).)

stick one, can be represented as different forms of sequential breakage process (see Section V.C.). The sequential breakage model which leads to the same result as the broken-stick model was termed the “MacArthur fraction model” (Tokeshi, 1990a). Indeed, species formation and invasion in ecological communities are more sequential, temporal processes than a spontaneous/simultaneous event, so the original conceptual formulation of the broken-stick model may be less suitable than the sequential process envisaged as the MacArthur fraction.

3. Evenness/Dominance Relationships

One aspect of species abundance patterns which seems to have attracted much attention is the steepness with which abundances decline from the most abundant species to the least abundant one within an assemblage. When relative abundance is plotted against species sequence, different models show different slopes. This is closely related to one of the diversity measures (evenness) which relates to how equitably species are distributed in terms of abundance. In communities where species show strong, sequential dominance, a steep slope will result, whereas those composed of species of similar competitiveness/resource use will be associated with a shallow

slope. Amongst four earlier models it is well known that evenness or uniformity of abundance increases in the order of geometric series, log series, log-normal and broken stick (Fig. 1(a)). Amongst stochastic niche-oriented models (see Section V.D), the dominance pre-emption model has the steepest slope and the dominance-decay model the shallowest (Fig. 1(b)). When different communities are compared, this aspect of species abundance patterns is often the easiest to demonstrate and the relevance of different models may be linked to such demonstrable differences. For example, successional communities may move from earlier stages where dominance is pronounced (steep slope) to later stages where relative abundances are more equitable (e.g. Bazzaz, 1975; May, 1981). It may be tempting to associate such a change with different models, implying different mechanisms of community organization. However, it should be noted that, although these changes may be real, they do not necessarily signify substantive change in the mechanisms of relative abundance as embodied by different models. Thus, caution needs to be exercised when a community appears to shift, for example, from the geometric-series model to the broken-stick model. If the patterns of evenness are the focus of analysis, there may not be much point in relying on a set of completely different models; simple application of a linear-regression model (i.e. the geometric-series model) to the rank versus log (abundance) graph will be sufficient for rough comparisons. Indeed, this is exactly what Motomura (1932) intended when he first proposed the geometric-series model; the slope of the regression indicates the 'complexity' of species composition in a community. Figure 2 shows the linear model being superimposed on the successional plant community data spanning 40 years (Bazzaz, 1975). Note that this does not entail an attempt to make goodness-of-fit comparisons, rather, the idea is to examine the evenness aspects of different communities on the basis of a simple, uniform framework. For this purpose the geometric-series model appears to be the simplest and the most straightforward of the models, and it is certainly advantageous to be able to rely on a model the parameter of which can cover a range of different situations. A similar philosophy was adopted by Kempton and Taylor (1976) who fitted the log-normal model to the above data from successional communities. The use of the geometric-series model for such comparisons may prove more meaningful than its interpretation as a model of allocating a fixed proportion of abundance k for successive species, as it has traditionally been treated in the literature. Using the geometric-series model in this way is logically more sound than the application of the broken-stick model to a single, unreplicated data set to indicate evenness of a community, as has been suggested by Magurran (1988). The geometric-series model can also be considered as an abstract, deterministic form of a family of more realistic, stochastic models including the dominance pre-emption and the dominance-decay models.

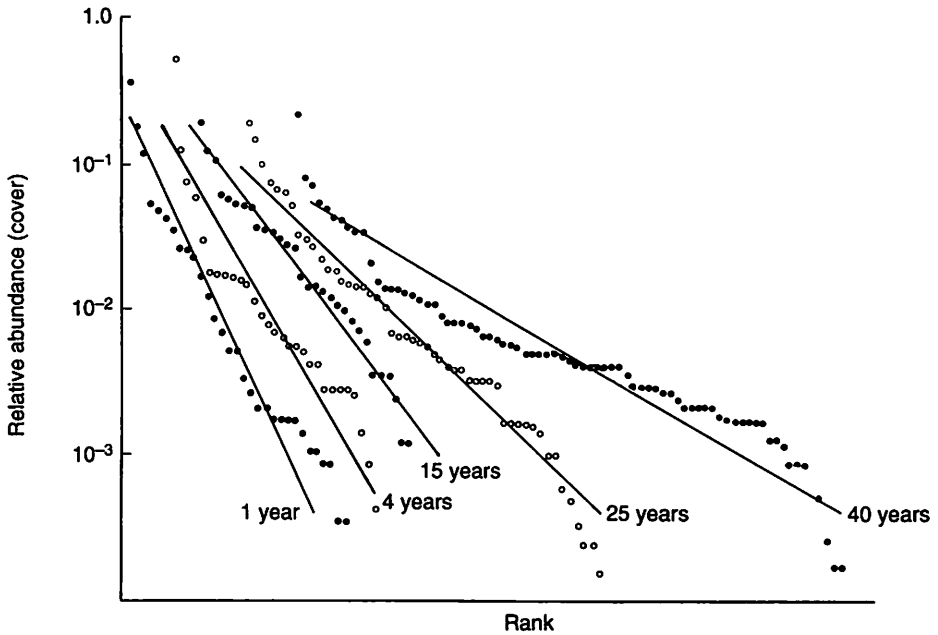


Fig. 2. Rank–abundance relationships of successional plant communities of the deciduous forest, representing five different ages after abandonment. Note the progressively shallower slope of the superimposed geometric-series model in older communities. (Adapted from Bazzaz (1975).)

D. Deterministic and Stochastic Models

Whilst the distinction between deterministic and stochastic models has widely been recognized in other areas of ecology such as population dynamics and predator–prey relationships, models of species abundance patterns have rarely received attention in this respect. This is partly due to the limited range of models proposed and their rather disparate nature, thus making it difficult to undertake a systematic development and comparison of deterministic and stochastic models within a single conceptual framework. With the recent consideration of stochastic niche apportionment models in terms of their application to real data (Tokeshi, 1990a), however, the aspect of stochasticity in species abundance models has been given more prominence.

Since organismal abundances are simultaneously influenced by several different factors, the incorporation of pseudo-random variation in a model is likely to represent some improvement in its reality. In addition, stochastic abundance models can accommodate the concept of sampling variation more easily than can deterministic models when comparisons are to be made with field data. On the other hand, stochasticity may partly be attribut-

able to our inability to distinguish and describe some processes within the system under study. Amongst the niche-oriented models listed in Table 1, all but the geometric-series model entail stochasticity. In the original formulations of the dominance pre-emption, the random-fraction, the MacArthur-fraction, the dominance-decay and the random-assortment models, stochasticity was incorporated as uniform randomness under the given constraints of each model (see Section V. C). It is of course possible to incorporate other types of randomness (e.g. normal distribution within a given range of variation). For example, Sugihara's sequential breakage model assumed that successive breakage points were located with a triangular probability distribution which Sugihara (1980) considered to fit well with some ecological data. The relevance and usefulness of incorporating this and other types of randomness in different models remain to be examined further using more data.

Although MacArthur's broken-stick model was presented as encompassing randomness, the aspect of stochasticity has virtually been ignored in the subsequent studies applying this model to data, with a notable exception of Webb (1974) who examined the statistical fluctuations of abundance values of this model. Indeed, failure to recognize the broken-stick model as a stochastic model stems from the original paper by MacArthur (1957), where the model was uncritically (i.e. without taking into account random variation in abundance values) compared with real data. In considering any stochastic species abundance model, the first point to realize is that abundances can only be expressed as expected average values which result from repeat observations and are subject to stochastic variation. It is meaningless to compare one observed value with the theoretical value that is expected to obtain as an average of many observations. Thus a single set of observed abundance values for a community is not sufficient for a rigorous test with a stochastic model. The problems of testing models are discussed in detail in Section VII.

Statistically orientated models such as the log series and the log-normal models are, in practice, treated as deterministic models with no variation allowed for frequency values, although in theory there is often an implication that they entail some stochastic processes. In the case of the log-series model, following Fisher *et al.*'s (1943) pioneering analytical work, Boswell and Patil (1971) and Watterson (1974) considered several hypotheses which lead to a log-series distribution. One of them concerns the randomization of time intervals with which species arrive successively to pre-empt a fraction k of the remaining niche (see Section V.C.1). Here, the model clearly defines a stochastic process involved, though its verification with real data may be hard to achieve. Indeed, the usual mathematical expression of the log series

$$S_n = \alpha X^n / n$$

should be interpreted as representing the *expected frequency* of a species with n individuals, implying that some stochastic variation exists around this value. A similar argument applies to the derivation of the log-normal model through the Poisson log-normal probability (see Pielou, 1975). Notwithstanding the inherent stochastic nature of the log-normal, Preston (1948), in the first attempt to test this model against field data, simply used expected frequencies to graduate and group the observed frequencies, thus effectively assuming that each species is represented by its expected number of individuals with no stochastic variation. Though Bliss (1965) considered such an approximation to be quite adequate, there is as yet no detailed study investigating the importance (or otherwise) of including stochastic variation in the analyses of statistically oriented species abundance models. It may well be that, because statistically oriented models generally specify not a single value but a range of abundance values to be realized by each species (i.e. grouping of expected frequencies to form tractable frequency classes), sampling variation is to some extent automatically catered for, and consequently the need to consider explicitly the aspect of stochasticity is reduced in comparison with niche-orientated models. Of course, this does not constitute a full justification for treating these models as if they were completely deterministic, and further investigation in this respect is necessary. Whether a model is regarded as deterministic or stochastic is particularly important when testing the fit with real data, a point which is examined later.

E. Presentation of Rank-Abundance Graphs: Towards Standardization

One of the confusing aspects which has surrounded the analyses of species abundance patterns concerns the various ways in which data are presented for visual examination. When different data sets are presented in different ways, cross-data comparison becomes an immediate problem, which partly accounts for the lack of comparative studies in this discipline. Indeed, four earlier models (the geometric series, the log series, the log normal and the broken stick) were each expressed by original proponents using different plotting schemes. The classification of these four models as statistically oriented models and niche-oriented models coincides with a major division with respect to the presentation of species abundance data. The first scheme of presentation adopted with the log-series, the log-normal and other statistically oriented models constructs frequency distributions by plotting frequencies (numbers of species) against number of individuals per species. In Fisher *et al.*'s (1943) original paper introducing the log-series model, the abscissa representing the number of individuals per species was expressed on the arithmetic scale (Fig. 3(a)), while for the log-normal model the log scale has generally been adopted (Fig. 3(b)) (normally to the base 2 as pro-

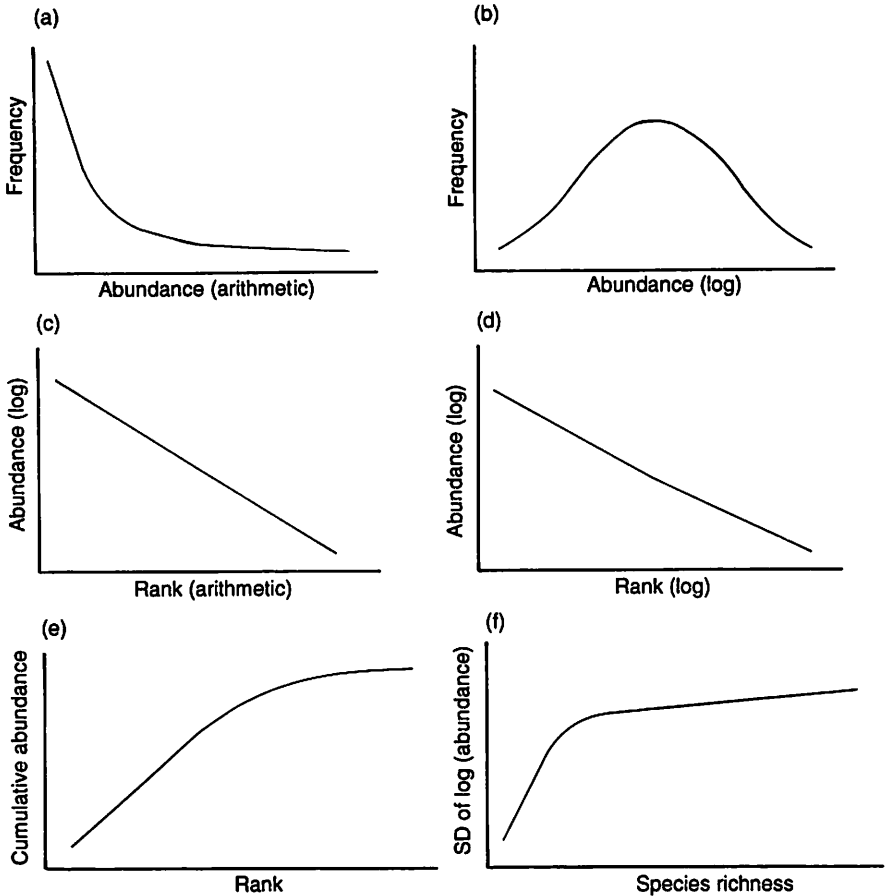


Fig. 3. Graphical presentation of species abundance data. (a, b) Frequency (number of species) plotted against the abundance (number of individuals per species) on the arithmetic (a) and the log scale (b); curves represent the log series and the log-normal, respectively. (c, d) Relative abundance (log scale) plotted against species rank on the arithmetic (c) and the log scale (d); lines represent the geometric series and the broken stick (or the MacArthur fraction), respectively. (e) Cumulative abundance plotted against species rank. (f) Standard deviation (SD) of log (abundance) plotted against species richness. Curves in (e) and (f) are hypothetical.

posed originally by Preston (1948), but the base 3 or 10 has sometimes been used (see Williams, 1964). In the second scheme of presentation associated with niche-oriented models, the abundance or number of individuals is plotted against the ranked order of species from the commonest to the rarest. MacArthur (1957) proposed the use of a log scale for rank (Fig. 3(d)), while the arithmetic scale has been used with the geometric series (Fig. 3(c)). Thus, there are four different methods of graphically presenting species abundance data (Fig. 3(a-d)), each associated with a different model.

Although not associated with any of the existing models, there is another method for graphical presentation which was originally proposed by Pielou (1975). Her aim was to enable a comparison of fairly similar communities with one another in order to determine whether their species abundance distributions tend to be of the same form even when the communities are far from homogeneous in species composition. This involves plotting percentage cumulative abundances (from 0 to 1.0) against species rank (Fig. 3(e)). This approach was also adopted by Patil and Tailie (1977) and Lamshead *et al.* (1983) who termed it as an "intrinsic diversity profile" and a "*k*-dominance curve", respectively. There is, however, no reason to consider that this plotting method is conceptually superior to other methods for demonstrating either diversity or dominance pattern of a community, and therefore it is perhaps more appropriate to use a simpler, neutral term ("cumulative abundance" graph). Apart from the difficulty of associating this plot with various models, there is as yet no way of statistically comparing more than two data sets plotted on a cumulative abundance graph, while two data sets (communities) can be compared using the Kolmogorov-Smirnov two-sample test. Platt *et al.* (1984) simply relied on visual inspection to compare curves on the graph, but the statistical validity of such an approach needs to be clarified. Furthermore, Warwick (1986) used this plotting method to compare two curves, one based on numbers of individuals and the other on biomass derived from a single community, to assess the effects of organic pollution in marine benthos (see Section VIII.C). Despite these attempts with marine data, theoretical justification for this method is thin and its usefulness remains to be seen.

If comparison is to be made between a range of data sets, the choice of a simple and versatile plotting method is very important. Between the two variants of frequency distribution plots used with statistically oriented models, it is better to use the one with the logarithmic abundance class (called "octave" by Preston (1948)) (Fig. 3(b)) than the arithmetic version (Fig. 3(a)), the reason being that the log scale can easily accommodate any model, whereas the log-normal model cannot neatly be expressed on an arithmetic axis. Comparing the two variants of the rank-abundance plots, the one with $\log(\text{rank})$ (Fig. 3(d)) has an advantage only with the broken-stick (i.e. the sequential MacArthur fraction) model in that the model appears as a nearly straight line. Thus the arithmetic rank versus $\log(\text{abundance})$ plot (Fig. 3(c)) is more convenient and versatile.

The frequency distribution plot is restricted to the use with large assemblages containing well over 30 species (preferably more; Preston (1957) suggested an adequate sample to be with approximately 200 species); otherwise the plot will be statistically meaningless and comparisons with other models cannot usefully be made. The rank versus abundance plot, however, can accommodate both small and large communities. Thus, with a homoge-

neous community containing a relatively small number of closely related species, the rank versus abundance plot is the only feasible approach. Considered altogether, if one method of presenting species abundance data is to be adopted in order to facilitate comparisons among different data sets, plotting logarithmic abundances against the arithmetic rank order (Fig. 3(c)) seems to be the most versatile approach. This may create a problem with testing statistically oriented models, but the advantage of presenting and comparing data (at least visually) on common grounds perhaps outweighs this slight disadvantage. On the other hand, if the communities to be analysed are all species rich, the frequency distribution plot with log (rank) (Fig. 3(b)) may be adopted; however, this does not necessarily facilitate statistical comparisons of different data. In such a case one possibility is to fit the log series (or the log-normal) model uniformly to all the data and to examine the variation in parameter values, irrespective of the goodness-of-fit of the model with some data (see Taylor, 1978; Kempton and Wedderburn, 1978). Note that this approach is similar to fitting the geometric-series model to a range of data on a rank versus abundance graph in order to compare evenness in communities, as mentioned earlier.

If a large number of communities is to be compared in terms of species abundance patterns, there is a possibility of another plot which may simplify such an exercise. Here, the standard deviation of the log (abundances) of each species in a community is plotted against total species richness (number of species). Thus, each community is represented on the graph as a single data point (Fig. 3(f)). This plotting method may be convenient for comparing a large number of different communities or a few communities with many replicates each, but it should be noted that this involves an important conceptual issue relating to global versus community-specific patterns (see Section VI.C). So far there have been very few studies in which this method has been used to present species abundance data (see Preston, 1962; Sugihara, 1980) and its use still remains to be explored. In particular, the relevance of using this plot to test the fit of different models and its discriminant power needs to be investigated.

V. NICHE AND SPECIES ABUNDANCE MODELS

A. Unit of Measure

The word "abundance" with respect to species abundance models has generally been interpreted to mean "number of individuals". Thus, the original papers introducing the four earlier models (the geometric-series (Motomura, 1932), the log-series (Fisher *et al.*, 1943), the log-normal (Preston, 1948) and the broken-stick (MacArthur, 1957) models) all relied on the number of individuals as the unit for expressing abundance. If the

term "abundance" is explicitly equated with the number of individuals and this usage of the term is uniformly accepted by ecologists, there would be no room for considering further the problems of the unit of measure in this discipline—i.e. the number of individuals is what "abundance" implies and that is it. In reality, however, there are a number of difficulties encountered if we always equate abundance with the number of individuals. Here, some considerations are given to practical as well as conceptual problems relating to this aspect.

If a species abundance model relates to some kind of division of resources as a basis of difference in abundances among members of a community, the number of individuals becomes an unsatisfactory measure unless individuals are of comparable sizes. When body size varies greatly among different species in a community, abundance as expressed by the number of individuals cannot logically be linked to resource division by species. Because body size varies between different species and within a population according to age and nutritional conditions, the number of individuals is unlikely to reflect with accuracy the level of resources required by a species population within a community. The problem then is whether or not the degree of inaccuracies associated with the use of numbers is high enough to invalidate comparisons among data and with models—an aspect which has not been touched on in the past.

Where substantial variation in size occurs, biomass reflects resource requirements more accurately than do numbers. Thus, biomass is preferable to numbers as a measure of abundance whenever models of resource apportionment are involved. In the present context it is most straightforward and convenient to treat biomass simply as encompassing all the body structures (including shells, exoskeletons, dead barks, hairs, etc.) unless there is a strong reason to believe that other treatment would make a far better representation for a particular comparison. Biomass is, in general, easier to standardize across different taxa, whereas the number of individuals may be difficult to express for colonial and modular/clonal organisms (Harper, 1977, 1981; Jackson *et al.*, 1985; Harper *et al.*, 1986; Hughes, 1988). Similarly, with small organisms counting individuals is often more time-consuming than is measuring biomass. On the other hand, objection can still be raised against the total reliance on biomass as an indicator of abundance, especially if numerous but small-bodied species must be described as "less abundant" than species with few but very large individuals. In the light of the above comments, perhaps the best approach for the time being is to use both the number of individuals and biomass in the analyses of species abundance patterns (see Tokeshi, 1990a). This will increase the amount of information available for a given community and, at the same time, facilitate comparisons across communities. Considering the implicitly acknowledged variation in body size within a community and the tendency to invoke the

concept of resource partitioning among species, it is remarkable that in the vast majority of empirical studies on species abundance patterns the number of individuals has only been used to quantify abundance.

Apart from the number of individuals and biomass, surface cover is frequently used as a measure of abundance with encrusting organisms such as barnacles, mussels, bryozoans and algae in marine environments as well as various plants in terrestrial environments (e.g. Mitchley, 1983). In most of these cases cover is presumably closely correlated with the number of individuals or biomass and is considered to reflect the pattern of division of the crucial resource (two-dimensional space).

If emphasis is placed on analysing patterns of resource division among species and on testing niche-apportionment models, it may be tempting to use a unit of measure other than numbers, biomass or cover which is considered to be more directly related to resource utilization for a given assemblage of organisms. For example, energy flow, productivity, calorific values, respiratory gas exchange rate or the amount of photosynthetic pigments may constitute more convenient and direct measures for resource-centred analyses. However, these measures cannot necessarily be linked to the idea of species *abundance* with ease, and therefore the investigation may depart from the original theme of analysing *species abundance patterns* in ecological communities. On the other hand, if research is focused on resource partitioning and interactions in general among a group of species, rather than on species abundance patterns in the narrowest sense, there should be no logical difficulty in adopting any unit of measure as deemed appropriate. It is therefore important to define the objectives of study before analysis is embarked upon; otherwise, the conceptual basis of the investigation can inadvertently be lost in the maze of analytical procedures.

In this respect it is notable that Whittaker (1965, 1975) has consistently used the term "importance", not "abundance", of species in a community. He defined "importance" as a group of measurements by which the species in a community can be compared, implying that any measure irrespective of whether it can be related to "abundance" or not, can be employed. Thus, in his own study of the forests in the Great Smoky Mountains, values of net production were used for comparisons of different species of plant, and what are now called "rank-abundance graphs" were described by him as "*importance-value curves*". As mentioned above, a term such as "importance" can conveniently be linked to the use of various measures, but if this is done the contact with the concept of abundance may inadvertently be reduced. In addition, the word "importance" tends to imply a value judgement, which may not be desirable in the descriptive phase of a work. Therefore, unless a clearly different research objective is proposed, it seems reasonable to refer to "species abundance patterns" and their measures.

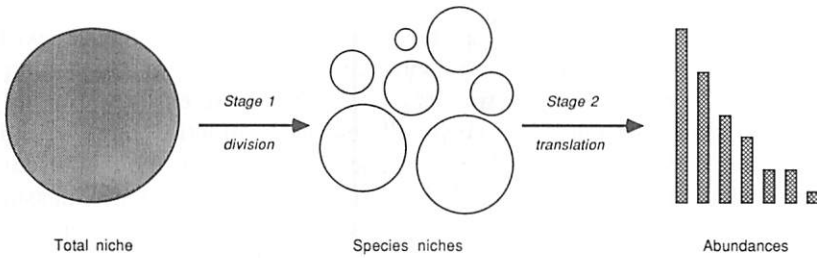


Fig. 4. Conceptual basis of niche-oriented models of species abundance.

B. Links Between Abundance, Resource and Niche Apportionment

The above issue concerning the choice of abundance measure in relation to the focus of investigation also relates to the fundamental problem of interpreting what a species abundance model is designed to deal with. Because abundance values *per se* of different organisms cannot be considered as a single entity, there is a logical need for a unifying background from which abundance values are derived. The basic line of argument is that abundances of different species within a community reflect the amount of resources secured by each species and, therefore, the patterns of species abundance can be explained by models describing processes of resource division among species. Here, the nature of resources involved is bound to vary from one community to another and cannot be specified. For this reason a more inclusive term relating to the overall needs of species existence, namely "niche", may be used to signify something to be divided among different species (see reviews by Whittaker (1972) and Schoener (1989) for the historical development of the concept of "niche"). Thus the problem of describing species abundance patterns is translated into the problem of developing niche-oriented models. This, however, leaves another issue concerning the link between resource/niche and abundances unresolved. Although this is an important issue, researchers have generally ignored it, tacitly assuming that the amount of niche secured by a species is more or less directly reflected in its abundance, whether expressed by numbers or biomass. As discussed in the previous section, a closer coupling between "niche" and "abundance" may in some cases be achieved if the latter is expressed by an unconventional measure other than numbers, biomass or cover, but this will crucially depend on the researcher's perception of "abundance"; such an interpretation may be too subjective to be accepted universally.

In order to facilitate understanding, the above discussion is represented schematically in Fig. 4. In the first stage the total niche is divided into species niches following some division rules. In the second stage species niches are translated into the abundance of each species. Models of species abundance

patterns, particularly niche-apportionment models, are designed to describe the first stage, whilst assuming that one-to-one correspondence exists between species niches and their abundances. The validity of this assumption is hard to prove, because species niche is an elusive entity to quantify in the first place, though it is conceptually useful. In practice, however, this assumption is deeply ingrained in the process of applying models to data because what can actually be handled with models is an abundance measure such as the number of individuals or biomass, not species niches. Thus, one-to-one correspondence between species niches and abundance values cannot effectively be questioned within this entire analytical scheme.

In relation to this, one aspect that has rarely been touched upon in studies of species abundance patterns concerns the distinction between fundamental niche and realized niche (Hutchinson, 1957, 1965, 1978). Despite the fact that Hutchinson's niche concept has had a huge impact on the development of modern community ecology in general (see Schoener, 1989), few researchers have examined in depth the possible implications of this concept for the analyses of species abundance patterns (e.g. Whittaker, 1972). From a theoretical viewpoint, rules of niche division as envisaged in niche apportionment models may be considered to relate more strongly to fundamental niche, which specifies species tolerance ranges within the multidimensional resource space. This, however, leads to a logical problem because realized niche, which would more directly relate to species abundances, might be so different from fundamental niche that the link between niche apportionment models and species abundance values is virtually lost. If, on the other hand, niche apportionment models are assumed to relate more closely to realized niche, or to the combination of fundamental niche and realized niche, this problem will not become too serious.

The above discussions notwithstanding, it is also meaningful to conceive of a model where there is no one-to-one correspondence between niche and abundance (see Section V.C.10). Such a model could reveal something about the organization of a community, not necessarily relating to the precise form of niche apportionment.

Conceptually, it is possible to treat models independently of the issue of species abundances and apply them to problems which are only indirectly related to abundances, such as energy partitioning patterns in a community. This approach concentrates on the processes of niche division without the need to consider the link between niche and abundance. Although there is as yet no study which has employed models in this way, this approach may turn out to be useful in terms of the overall development of community ecology, not confined to the analyses of species abundance patterns *per se*.

Statistically oriented models, as opposed to niche-oriented models, may be considered as being free from this intricate logical relationship, dealing directly with abundance values themselves. If the objective of a study is

purely to make a statistical description of the species abundance patterns, this will be a valid argument. If, on the other hand, any biological explanation is to be attached to the fit of a statistically oriented model, the aspect of niche-apportionment is unlikely to disappear since it is difficult to deny that niche is the basis of species abundances, especially when a multi-species system is dealt with.

Consideration of the conceptual basis of analysing species abundance patterns points to the importance of dealing with a community the members of which possess a similar niche in order to ensure that common total niche is subdivided among species, as depicted in Fig. 4. As more and more dissimilar organisms are considered together as a community, a common niche base is lost and the situation inevitably approaches a collection of unrelated elements the structure of which is dictated by statistically large numbers. This situation will of course be aptly described by statistically oriented models, but the biological meaning of such an exercise is open to question. This point is discussed further in Section VI.

C. Development of Niche-oriented Models

As discussed above, niche-apportionment models are supposed to play a vital role in the linkage between the niche concept and realized species abundances. Thus the development of niche-apportionment models has a close bearing on the exploration of biological processes involved in species abundance patterns. Interestingly, despite possible ecological importance, niche-apportionment models have not received as much attention as statistically oriented models have. This is partly due to the fact that the relevance of the concept of niche-apportionment in the studies of species abundance patterns has been slow to be recognized, and new models of niche apportionment have been proposed only recently. In addition, species-rich samples such as those of marine benthic communities tend to "condition" researchers to rely on statistically oriented models which earlier proponents have demonstrated the use of. It is therefore considered worthwhile to make a systematic review of niche-apportionment models here.

1. Geometric-series Model

The geometric-series model as a niche-apportionment model stipulates that the first species takes a proportion k of the total niche, the second species takes the same proportion k of the remaining niche, and so on (Fig. 5). Because k is fixed for all species, a strict interpretation of the model implies that deviation from a single value of k is due entirely to sampling errors and environmental noise, while k remains invariable. The model has been known to fit small communities, but this may simply be the result of

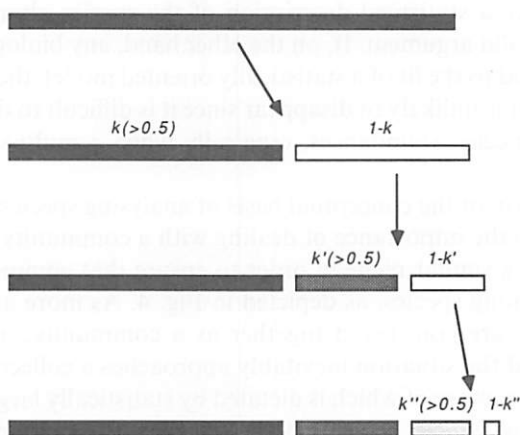


Fig. 5. Schematic representation of the geometric-series model.

fewer data points representing different species on the rank–abundance graph, giving an impression of less deviation from a linear regression than large communities with many data points. Statistical evaluation of the fit of this deterministic model (all other niche-orientated models are stochastic) to data is rather elusive and is discussed in Section VII.A.

2. Broken-stick Model

MacArthur's (1957) analogy of placing $n - 1$ points randomly on a line of unit length and simultaneously breaking it at those points into n lengths (Fig. 6) can be rephrased as a group of n species of equal competitive ability simultaneously occupying the total niche and jostling each other to determine niche boundaries. By implication, the model is applicable to a relatively small community of closely related species which has reached an equilibrium state. Communities of chydorid cladocerans as revealed by sediment core samples from a post-glacial lake seem to approach this model

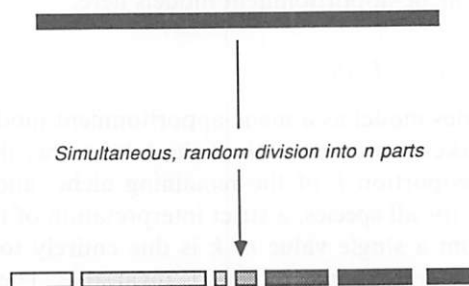


Fig. 6. Schematic representation of the broken-stick model.

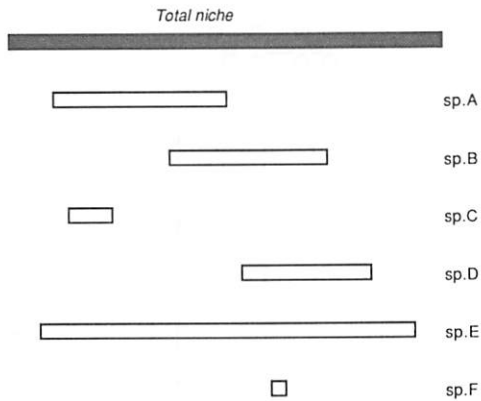


Fig. 7. Schematic representation of the overlapping-niche model.

with the progression of time (Goulden, 1966). A similar example of cladoceran communities was found where volcanic eruptions interrupted the community development twice during the last 12 000 years, but each time the broken-stick distribution was approached as time passed (Tsukada, 1972). Despite these and other examples (see King, 1964), there are problems of testing the fit of this model to data.

3. *Overlapping-niche Model*

According to MacArthur (1957), the abundance of any species is determined by the distance between a pair of points thrown at random onto a stick of unit length (Fig. 7). The implication is that species niches can overlap to any extent and yet they share the same total niche space, which is logically incoherent and may only be approximated by a transient community with superabundant resources. The model has not been formally tested against real data.

4. *Particulate-niche Model*

This model stipulates that species in a community share a fixed total number of units of abundance ("niche particles"), based on the random allocation of units among species, i.e. each species has an equal probability of receiving a unit (Fig. 8). As the total number of units to be allocated increases relative to the total number of species, all species approach an equal abundance. Thus this model represents a community of inherently equitable species, more so than the broken-stick model. All the species are assumed to have the same rate of population growth and competition does

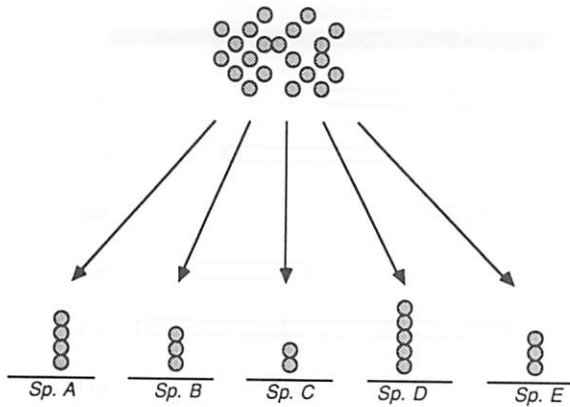


Fig. 8. Schematic representation of the particulate-niche model.

not occur once a niche is occupied. Theoretically this leads to a Poisson distribution of species abundances.

5. Dominance Pre-emption Model

This is a type of sequential niche breakage model where species successively pre-empt a dominant portion (> 0.5) of the remaining niche (Fig. 9). The first, competitively most superior, species takes more than half of the total niche, and the second species takes more than half of what is remaining, and so on. This process guarantees the dominance of a species over all the later species combined, and the dominance hierarchy is fixed. In Tokeshi's (1990a) original version of the model the portion to be carved out by each

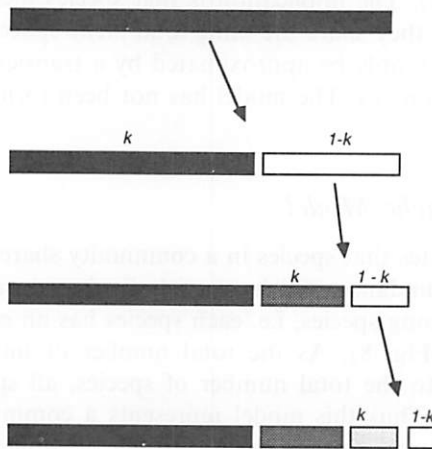


Fig. 9. Schematic representation of the dominance pre-emption model.

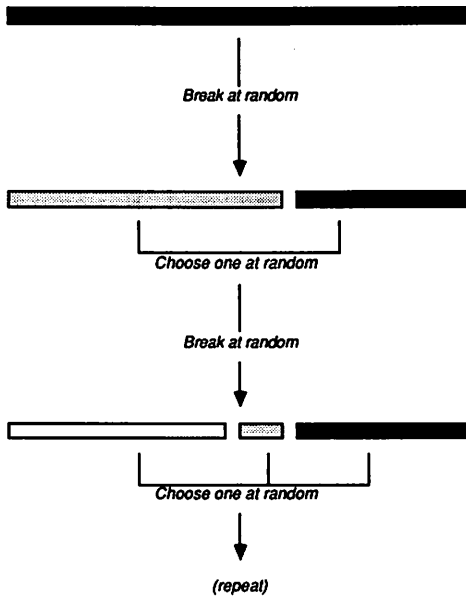


Fig. 10. Schematic representation of the random-fraction model.

species was assumed to be determined randomly (uniform) between 0.5 and 1.0, meaning that expected abundance values approach the geometric series with $k = 0.75$.

6. Random-fraction Model

This sequential breakage model involves two-stage random processes (Fig. 10). Firstly the total niche is divided at random into two portions, and secondly one of the two is chosen at random for the second division. The resultant three portions are then subjected to random choice and division. Thus, a newly colonizing species is supposed to invade the niche of any species and takes an arbitrary proportion of it. Numerical abundances of freshwater chironomids appear to fit this model (Tokeshi, 1990a).

7. Sugihara's Model

Sugihara's (1980) sequential breakage model was originally proposed as giving a biological explanation to Preston's (1948) canonical log-normal model. Here, it is worth treating this model separately and clarifying its relationship with other niche-apportionment models. In essence, this model is considered as a special version of the general random-fraction model.

The process of niche division envisaged by Sugihara (1980) was basically

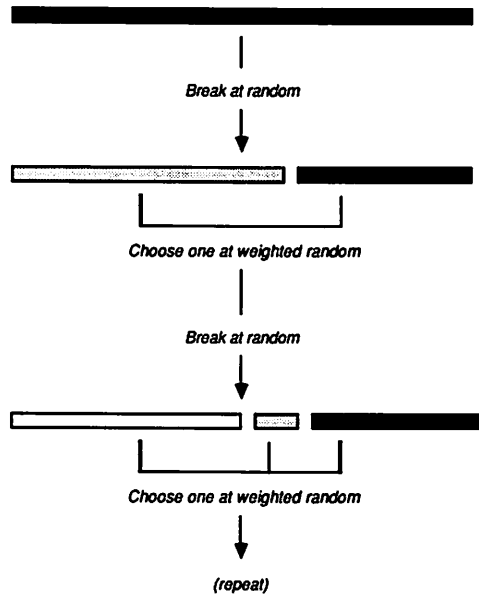


Fig. 11. Schematic representation of the MacArthur fraction model.

the same as that in the random-fraction model, with the total niche successively divided into smaller portions through random choice and division. The only practical difference between the two models concerns the form of randomness associated with the determination of breakpoints. In Sugihara's model a triangular frequency distribution between $p = 0.5$ and 1.0 with a peak at $p = 0.75$ was assumed, following an examination of a couple of experimental data sets on species dominance and competition, whereas the random-fraction model uses a uniform random distribution between $p = 0.5$ and 1.0 , as mentioned above.

Although Sugihara (1980) emphasized the aspect of multi-dimensional niche in his model and used the analogy of a stone being successively broken into pieces (see Epstein, 1947; Aitchison and Brown, 1966), there is nothing concrete about multi-dimensionality which separates his model from other niche-apportionment models; his own calculation will not be affected by single- versus multi-dimensionality. It is important to note that a niche, as referred to in niche-apportionment models, is implicitly assumed to be multi-dimensional, being the sum of resources and factors which affect species existence. The analogy of a stick or a stone is no more than a figurative representation of a niche and should not be interpreted as implying differences in dimensionality, as has sometimes been done in empirical studies as well as in reviews.

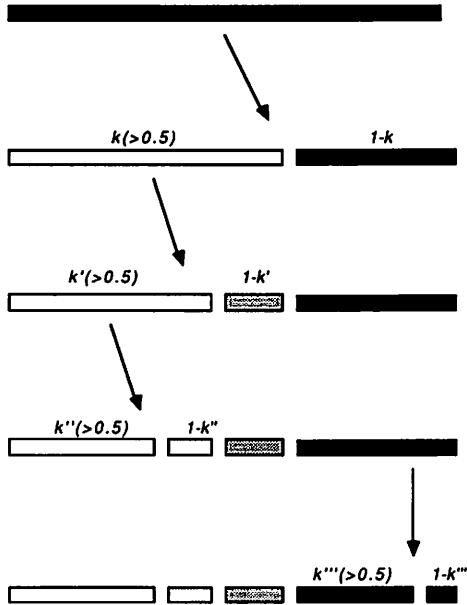


Fig. 12. Schematic representation of the dominance-decay model.

8. MacArthur Fraction Model

This model stipulates that total niche is divided at random and one of the two resultant niches is then chosen with probabilities corresponding to the niche sizes, and subjected again to a random division. One of the three niches is then chosen in a probabilistic manner for a subsequent division, and so on (Fig. 11). In other words a new species is likely to invade the niche space of more abundant species in this model, whereas niches of different sizes have the same probability of being invaded in the random-fraction model. This model produces the same result as the broken-stick model of MacArthur mentioned earlier, but stresses the sequential, as opposed to simultaneous, process which logically places the model in a common framework with other models of this type. Furthermore, sequential processes are more congenial to evolutionary phenomena than to simultaneous ones. Indeed, earlier examples of temporal changes in cladoceran communities (Goulden, 1966; Tsukada, 1972) may be more appropriately represented by the sequential process envisaged in this model, rather than by a simultaneous process.

9. Dominance-decay Model

This model is an inverse of the dominance pre-emption model, stipulating

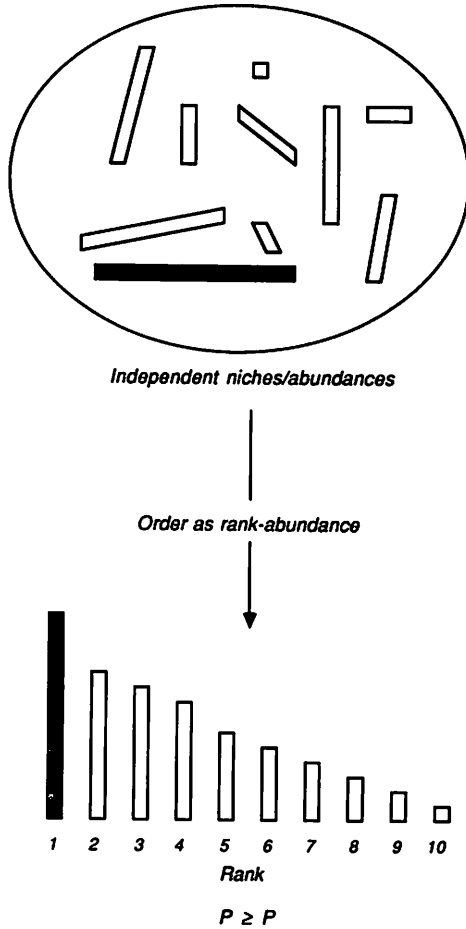


Fig. 13. Schematic representation of the random-assortment model.

that the largest niche in an existing assemblage is always subjected to a subsequent (random) division (Fig. 12). Thus, an invading species is supposed to colonize the niche space of the most abundant species in an assemblage. Dominance is always negated in this model, whereas dominance pre-emption always guarantees it. This process results in more equitable species abundances than expected from the MacArthur fraction (broken-stick model). Indeed, four sequential niche-apportionment models (dominance pre-emption, random fraction, MacArthur fraction and dominance decay) can be neatly classified according to the probability that the largest niche in an assemblage is subjected to subsequent division. Such probability decreases in the order: dominance decay–MacArthur fraction–random fraction–dominance pre-emption.

10. *Random-assortment Model*

This model refers to a situation where abundances of different species vary independently of each other (Fig. 13). This could occur either as a result of non-correspondence between niche apportionment and species abundances (see the disruption of the second stage in Fig. 4), or as a non-hierarchical, dynamic apportionment of niche in a variable environment. In the former case, patterns of species abundance do not reflect underlying niche apportionment for a variety of reasons, whatever form niche apportionment may take. The latter case occurs if the total niche of a community does not stay constant in size but undergoes variation, and each species carves out its own niche independently of other species on a temporally variable basis. Because of continual change in total niche, species are unlikely to saturate the niche most of the time (see Simberloff, 1981; Lawton, 1982; Walker and Valentine, 1984) and individual species niches are always subjected to temporal variation. In such a system there is not enough time for resource-based competitive interactions to develop, thus denying the fine-tuning of species niches within a total niche space. Mathematically the model behaves as a stochastic analogue of the geometric-series model with $k = 0.5$ (Tokeshi, 1990a).

A slightly different, alternative formulation of this model based on a sequential niche division is that the first species takes an arbitrary proportion of total niche and the second species again takes an arbitrary proportion of the remaining niche, and so on. Although this implies successive niche pre-emption, competitive relationships cannot logically be invoked here because the niche is assumed to be unsaturated (i.e. an invading species rarely occupies *all* the remaining niche) in this system. In all practicality, this is essentially the same as saying that species niches are mutually unrelated.

Caswell's (1976) neutral model, though not framed in the context of niche, can be considered similar to this model in that different species are assumed to be independent of each other.

11. *Composite Model*

It is not unlikely that a community encompasses two or more separate assembly rules, rather than only one. Tokeshi (1990a) suggested that the most plausible case would be that a few abundant species (e.g. up to the third most abundant in an assemblage) behave on the basis of niche apportionment, while the other less common species follow a random assortment, as envisaged in the previous model. Thus a composite model can be built up as a combination of, for example, one of the niche-apportionment models and the random assortment model (Fig. 14).

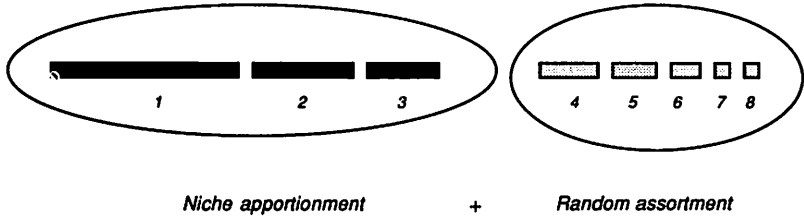


Fig. 14. Schematic representation of the composite model.

D. Species Abundance and the Density–Body Size Allometry

One of the issues closely allied to the concept of niche apportionment is how equitably resource/abundance is distributed among species in a community. A descriptive aspect of this issue has already been dealt with in Section IV.C. Here, attention is drawn to its functional aspects, including the recent controversy surrounding what is called the “density–body size allometry”.

Based on a logic of allometric relationships, Harvey and Godfray (1987) suggested that species abundance as expressed by biomass has a more equitable pattern (i.e. smaller variance) than that expressed by number of individuals (i.e. density). Sugihara (1989), however, found an error in their argument and suggested instead that the equitability or variance of species abundances in a community would be roughly the same for numerical and biomass data. If Sugihara’s suggestion is correct, the choice of a measure of abundance (see Section V.A) is simplified and analysis can equally be carried out using measurements based on either number or biomass. For a chironomid community, Tokeshi (1990a,b) demonstrated that the variance of $\log(\text{biomass})$ is larger than that in $\log(\text{number})$ (Fig. 15), implying that both Harvey and Godfray’s (1987) and Sugihara’s (1989) arguments are inappropriate. Furthermore, Pagel *et al.* (1991), whilst acknowledging their earlier error, showed that variance in biomass is in general larger than that in numbers. However, the fact that biomass is less equitably distributed than numbers in a community cannot necessarily be taken as proof of the existence of an allometric relationship between density and body size (Tokeshi, 1990b). As a measure of a three-dimensional entity, biomass is inherently more variable than number when applied to organisms with variable body size.

Damuth (1981, 1987) examined a variety of mammal and other animal species and demonstrated that population abundance (density N) changes allometrically with body size (weight W) such that

$$N \propto W^{-x}$$

where the allometric exponent x typically assumes a value of less than 1 (see Peters, 1983). Although this relationship was originally derived from a col-

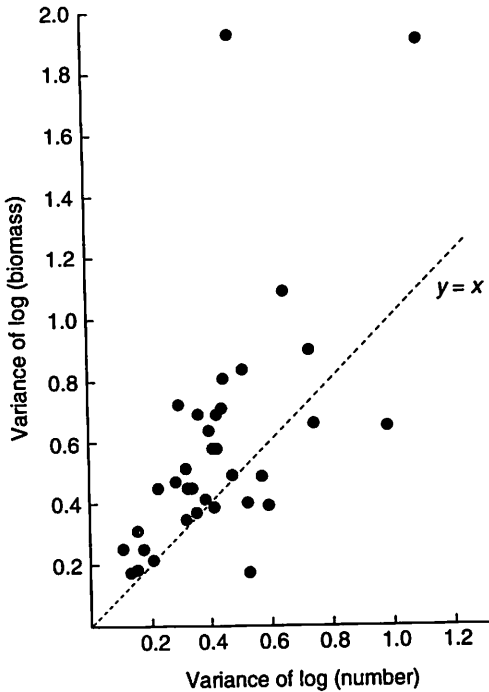


Fig. 15. Comparison between the variance of log (biomass) and variance of log(number) in a chironomid community. The former is significantly larger (binomial test, $p < 0.05$) than the latter. (After Tokeshi (1990a).)

lection of unrelated species occurring in different habitats, and hence belonging to different communities (Damuth, 1981, 1987), and subsequently supported by a number of other studies similarly spanning many taxa and a large range of body sizes (Peters and Wassenberg, 1983; Peters and Raelson, 1984; Juanes, 1986; Marquet *et al.*, 1990), it is tempting to infer that the same pattern may occur among species within a community or guild, thus allowing the explanation of species abundances simply through their body sizes. The limited range of data that has been published to date, however, seems to indicate that the relationship does not invariably exist within communities. Brown and Maurer (1986, 1987) and Tokeshi (1990b) found very weak or no relationship between density and body size for guilds of North American birds and freshwater chironomids in an English river, respectively. Furthermore, Juanes (1986), Brown and Maurer (1986, 1987), Gaston (1988), Gaston and Lawton (1988), Morse *et al.* (1988), Lawton (1989) and Blackburn *et al.* (1990) have all suggested that decrease in density with body size within communities may be much smaller than the value ($x = 0.57$) shown by Damuth (1981, 1987), or even undetectable. If

Damuth's result with $x = 0.75$ refers to density maxima of organisms rather than to average densities of most of the natural populations, actual values of density are more likely to fall below the line defined by

$$\log N = c - x \log W$$

where c is a constant. These circumstances would make the detection of a significant relationship more difficult against the environmental noise and sampling errors.

Damuth (1981, 1987) himself stated that the density-body size allometry may not apply to a group of organisms whose body sizes cover a relatively narrow range, which is generally the case with a single trophic guild or an assemblage of taxonomically related species. Furthermore, Tokeshi (1990b) pointed out that one of the difficulties of the allometric hypothesis relates to the nature of body size. Although body size is a relatively straightforward concept for most mammal and bird species which maintain a more or less the same, largely genetically predetermined, size through a large portion of active feeding life (i.e. the adult stage), it is a rather elusive trait for a population of organisms which undergo a steady or dramatic change in size throughout their life cycle. This applies in particular to species with indeterminate growth (e.g. marine invertebrates and fish) and those with active feeding life mostly restricted to the growing, juvenile stages (e.g. freshwater insects). For these and other organisms, body size within a population is not only a species-specific but also a strongly time-dependent character. The variable body sizes observed in many trophic guilds and communities make the basis of the allometric hypothesis less convincing, especially when resource utilization patterns in closely related species are to be analysed.

The energy used E by a population per unit time and area can be expressed as the product of M , the rate of metabolism which scales with body size ($M \propto B^y$), and density N :

$$E = MN \propto B^{y-x}$$

where y has been shown to be approximately 0.75 (Elgar and Harvey, 1987; Nagy, 1987; McNab, 1988). If the value of $x = 0.75$ suggested by Damuth (1981, 1987) applies to a particular community, the energy used by a population will be independent of body size ($E \propto B^{0.75-0.75} = B^0$), implying that species of different sizes within the community utilize exactly the same amount of energy. Obviously, if $y > x$ the energy usage increases with body size, while if $y < x$ the opposite is true. Consequently, that density is not related to body size (i.e. $x \approx 0$) indicates that energy use in a community is highly inequitable; species with large body size tend to command a disproportionately large share of resource use in the community. This seems to be the case with some terrestrial communities (Blackburn *et al.*, 1990), a fresh-

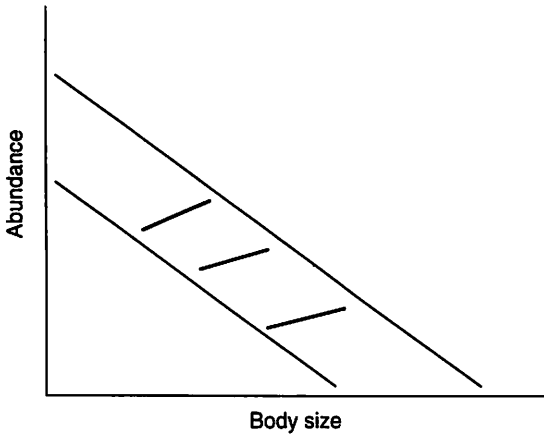


Fig. 16. Schematic representation of the relationship between abundance and body size in 147 species of breeding birds in Britain analysed by Nee *et al.* (1991). Birds on the whole demonstrate a declining abundance with body size where the slope approximates -0.75 (band delineated by two parallel lines), but within lower taxonomic groupings (tribes and genera) abundance more often than not increases with body size (short lines inside the band).

water chironomid community (Tokeshi, 1990b) and communities in general (Lawton, 1989). Recently, however, Nee *et al.* (1991) examined data on 147 bird species in Britain and found that abundance decreases as the -0.75 power of body size, indicating energy equivalence among species of different body sizes. Interestingly, they also found that abundance tends to increase with body size (i.e. inequitable share of resources) within lower taxa such as tribes and genera, suggesting that phylogeny has an important bearing upon this relationship (Fig. 16). Thus it appears that the issue is in need of further analyses, particularly with different taxonomic groups and in different geographical regions.

VI. DESCRIPTION AND INTERPRETATION

A. Model-free Description?

A range of models proposed to date and studies involving those models may give an impression that species abundance patterns can usefully be investigated only through comparison with models. It can be argued, however, that species abundance data need not be linked to any of the models (indeed, none may fit a particular data set), and it is perfectly legitimate to present species abundance data without recourse to models. If species abundances are dependent on the relative abundance of different resources which are in turn influenced by a range of loosely related factors, specifying a niche-

division rule (i.e. model) may not be a particularly illuminating exercise. Even if model fitting is not intended, species abundance patterns can be graphically presented on a rank–abundance diagram, which is useful for demonstrating the dominance pattern within a community (e.g. Hawkins *et al.*, 1982); the rank–abundance diagram can handle community data irrespective of numbers of species involved, whereas the abundance–frequency diagram is valid only for communities containing large numbers of species (see Section IV.E). If converted to the cumulative abundance plot (see Section IV.E), two sets of data can be tested against each other to see whether they represent the same species abundance pattern or not using the Kolmogorov–Smirnov two-sample test. For this to be meaningful, however, it is important to guarantee that the two data sets are gathered using a similar, standardized sampling procedure; even with a single community different sampling efforts could result in apparently different patterns of species abundance.

Where species abundance data are derived from a large number of similar habitats/communities (e.g. deciduous forests, coral reefs, rivers, grasslands, etc.), it is possible to perform multivariate-type analyses (see Gauch, 1982). For example, Hinch *et al.* (1991) used multivariate ordination techniques to examine the relationship between the species abundances of fishes in North American lakes and biological/abiological factors and biogeographical processes. In most situations the use of abundance data in this type of analysis is likely to provide more information on community patterns than is possible with presence/absence data (see Rahel, 1990).

Notwithstanding the arguments presented above, it is still worthwhile to attempt comparisons with models even for purely descriptive purposes. For example, results of multivariate analysis of species abundance data may be strengthened by explicit comparisons with species abundance models. Such an exercise is more likely to expose characteristics of the community concerned than does a simple presentation of data. The objective here is not to fit a particular model to data but to explore possibilities of description and interpretation through model-fitting exercises. It is at least a gain in knowledge if, after a rigorous examination, none of the models is found adequately to fit a given data set, thus opening up other possibilities. The majority of past studies, however, fall short of such a comprehensive analysis of species abundance patterns. This section reviews some aspects of pattern description and interpretation that have important implications, and yet have received inadequate attention so far.

B. Description and Mechanisms: Neutrality, Ambiguity and Possibility

One of the advantages of applying models to species abundance data relates

to the convenience of summarizing data with a limited number of parameters. This is particularly the case with statistically oriented models such as the log-series and the log-normal models which are suitable for communities with relatively large numbers of species. The first of the niche-apportionment models (the geometric-series model) was also proposed simply as a convenient descriptive statistic rather than as an explanation of niche-division processes among species. If convenience in description is sought after, the match between model and data can be relegated to a secondary consideration, and a model can be approximately fitted to a range of data sets, thus allowing comparison of parameter values pertaining to different data sets. In theory this is a valid approach, as long as the properties of the model are thoroughly known and parameter values are clearly linked to community characteristics. In this respect the geometric-series model is the most straightforward one, with the parameter k being related to the equitability ("complexity" in Motomura's (1932) original paper) of a community. In a similar vein the log-series model has been used extensively by investigators at the Rothamstead Experimental Station, England, with its parameter α being termed the "index of diversity" (Williams, 1954; Kempton and Taylor, 1974, 1976; Taylor *et al.*, 1976; Taylor, 1978). Parameters of the log-normal model, on the other hand, are less clearly linked to community trait(s), and there is some difficulty in using this model as a descriptive tool.

In general, description of patterns by means of a model is more meaningful if the model is based on clearly defined community processes, which would help elucidate underlying mechanisms producing patterns. In this respect statistically oriented models are at a disadvantage, because they are in principle not intended to represent particular ecological processes. Thus, these models may serve as a description, but not as an explanation. At the same time, it is notable that there is also an opposing view which emphasizes that the ecological neutrality of statistically oriented models allows useful quantitative description of patterns (see Southwood, 1987). This argument, however, is harder to justify, because what is regarded as the "neutrality" of statistically oriented models largely comes from the "ambiguity" of models with respect to underlying mechanisms and processes. The fact that a model such as the truncated log-normal model fits a range of community data may reveal nothing ecological but simply the model's flexibility in taking different forms (Fig. 17). Under these circumstances it is very difficult to attach much biological meaning to any variation in parameter values of these models. Thus, meaningful quantification with statistically oriented models is more often an illusion than a reality.

Amongst statistically oriented models, the log-normal model in particular is considered to be useful in describing ecological communities, having been found to fit a variety of ecological data (Preston, 1948, 1962; Williams, 1953, 1964; Whittaker, 1965, 1972). On the other hand, mechanisms leading to a

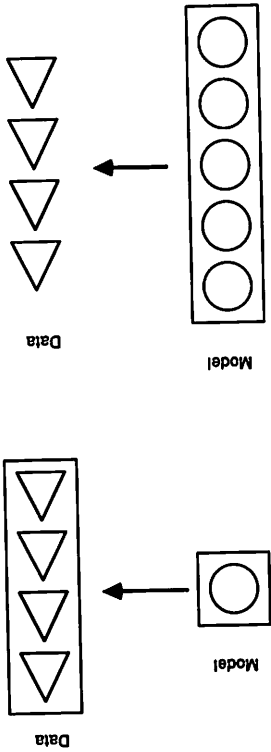


Fig. 17. The problem of relying on a model with an ambiguous mechanistic background. When a model fits a number of data sets (represented by triangles, upper diagram) from different communities, it is tempting to conclude that these communities are governed by the same process underlying the model (i.e. the circle inside the square). With statistically oriented models it is more likely, however, that a model fits a variety of data sets because it encompasses different processes (lower diagram) and hence is flexible enough to assume different forms. In such a case the fit of a model to different communities perhaps reveals more about the model's characteristics than about those of the communities.

log-normal pattern are at best obscure, with a multitude of propositions ranging from largely statistical (MacArthur, 1960; May, 1975; Ugland and Gray, 1982) to biological (Sugihara, 1980). A similarly ambiguous situation exists for the log-series model (see Fielou, 1969; Boswell and Patil, 1971). The point to be noted, however, is that as long as a (strong) possibility remains that the model simply results from statistical large numbers (the central-limit theorem), an attempt to offer an alternative, biological explanation for the model cannot logically be successful; statistical artefacts will lead to a log-normal pattern, irrespective of any biological process which may be involved. Under these circumstances it is meaningless to argue for a biological process as a separate mechanism producing the log-normal model. Only

when the possibility of statistical artefacts is clearly eliminated will it make sense to suggest a biological process as an alternative. Unfortunately, no study attempting to explain the log-normal model has adopted such a rigorous analysis.

If the fit to a model is generally improved as the sample size increases (i.e. a larger assemblage with less well-defined boundaries), the role of the central-limit theorem needs to be suspected, and any variation in parameters cannot reliably be interpreted to represent a substantial change in community structure, apart from a purely numerical effect. In this sense, a real challenge to using statistically oriented models in the analyses of species abundance patterns is how much useful information that is independent of statistical artefacts can be gained from a given set of data. For this it will not be sufficient to fit a model to observed data; in addition, investigation of model behaviours under relevant numerical conditions, perhaps involving simulation, is likely to be very important.

In comparison with statistically oriented models, niche-oriented models are generally free from statistical artefacts, although this does not necessarily mean that only a single interpretation of a model is possible. On the contrary, most niche-oriented models allow a number of different interpretations, although these differences are relatively slight compared with various propositions made for a statistically oriented model such as the log-normal model. One of the advantages of niche-oriented models is that, with the recent proposition and review of models of this kind, these models together encompass a range of species abundance patterns with subtle differences among them (see Section V.C. and Fig. 1(b)) which might occur in real communities, thus enabling a finer classification of patterns than is generally possible with statistically oriented models.

The fact that niche-oriented models encompass seemingly well-defined processes does not guarantee that communities which fit a model are governed exactly by the processes as embodied in the model. Rather, a good fit simply indicates that the processes thus depicted cannot be negated for the community concerned at the current level of knowledge. In the absence of one-to-one correspondence between process and pattern, a single fit of a model to data amounts at most to a suggestion of processes involved, never a proof. In this respect it is worth subjecting the same community to different types of analysis of community structure to see whether similar conclusions emerge from them. If all the analyses point to the same conclusion, the relevance of processes specified by a species abundance model would be enhanced greatly.

Faced with the difficulty of interpretation some authors opt for a view that species abundance models are better considered simply as a statistical description of patterns (see Magurran, 1988), thus reversing an earlier attempt initiated by MacArthur (1957) to conceive a way of describing pat-

terms on the basis of biologically based hypotheses rather than statistical ones. Although biological interpretation can never be straightforward, it is still worth seeking such possibilities whilst acknowledging that real systems are unlikely to operate precisely as a model suggests. The bottom line of this argument is that it is more profitable to leave some room for considering the biological background of species abundance patterns rather than relegating them to be always considered as a subject of statistical description. In this respect, that models do not necessarily specify a single mechanism but suggest a range of closely allied possibilities, particularly in the case of niche-oriented models, should be taken as a significant starting point, rather than as the failure of models.

C. Global versus Community-specific Patterns

In terms of describing and interpreting species abundance patterns by means of models, there are broadly two fundamentally different views. One is to regard the study in this discipline as a search for a global pattern among a diverse array of communities, with an expectation that a single model of species abundance can encompass the majority of, if not all, communities. The other view does not assume the existence of a global pattern, at least in the first instance, and treats patterns as being specific to different communities. Earlier investigators often adopted the former view, and in particular the proponents of different models tended to put forward a particular model as being capable of fitting a large number of data sets, thus implying that the model in question is globally applicable and that such a global pattern exists across different communities. This was clearly the case with Sugihara's (1980) work where he proposed a hierarchical niche-division model (see Section IV.C.6) as a basis of many ecological communities, thus terming it the "minimal community structure". Sugihara plotted the variance of abundance against species number for a variety of communities, demonstrating that data points are scattered around the curve expected from his model. One of the problems of this approach is that the division rule which Sugihara envisaged encompasses two extremes of the family of niche apportionment models, namely the dominance pre-emption and the dominance-decay models (see Fig. 1(b)). Thus data points representing different communities are naturally expected to lie between these, centred around the random fraction. Under these circumstances it is impossible to distinguish a situation where a single model applies globally to different communities from the situation where each community is governed by a different mechanism as embodied by different niche-apportionment models. This ambiguity is partly derived from the general tendency in this discipline to rely on unreplicated data, which makes it easier to direct research towards seeking global patterns while conveniently ignoring intercommunity differ-

ences. Clearly, there is a danger in attempting to find a global pattern, in that what is likely to be recognized as a global pattern may be too trivial or vague to be of interest ecologically. For example, a suggestion that communities follow some form of hierarchical niche division does not in itself represent a significant advance in our knowledge of how communities are organized.

In the light of the above comments, a more rigorous approach is to treat different communities as separate entities, each of which is considered to represent a different species abundance pattern. If this leads to the discovery of a non-trivial pattern (i.e. a pattern free from statistical effects of large numbers) across different communities, this will constitute firmer evidence of a global pattern of species abundance in ecological communities. It is perhaps more likely, however, that patterns of species abundance vary from one type of community to another, and indeed the elucidation of such variations is undoubtedly an important part of community ecology. Thus, from a strategic point of view the community-specific approach to species abundance patterns appears to be more fruitful and scientifically sound.

D. Contemporary and Evolutionary Processes

In interpreting models of species abundance patterns, one of the important aspects concerns the time-scale of processes involved. The processes of niche apportionment as described for various models in Section IV.C can be projected to community development either within a relatively short, contemporary period of time or over a long, evolutionary time. The former takes the view that the basis of species abundance patterns is a currently on-going process of niche division among species, including habitat colonization, local extinction and various forms of species interactions. In contrast, the latter emphasizes the importance of evolutionary processes as determinants of overall species abundance patterns currently observed in nature. In reality, however, the distinction between contemporary and evolutionary perspectives may not be clear-cut, there being a range of intermediate situations. This is inevitable since species abundance patterns are the product of evolutionary as well as contemporary processes, and the relative importance of these two is likely to vary among communities. Contemporary processes may be more important among organisms with relatively short life cycles which must colonize habitats anew in every generation, while evolutionary processes may have a stronger influence among long-lived species with overlapping generations. Another way of interpreting this issue is that evolutionary processes determine the fundamental niche (*sensu* Hutchinson, 1957), whilst contemporary processes operate on this fundamental niche to produce a realized niche. Despite its obvious importance, there is virtually no empirical study on species abundance patterns which has explicitly considered this issue and, therefore, ambiguity remains as to what time-scale

should be envisaged of niche apportionment for a given community. Some studies, such as Whittaker's (1975) examination of successional communities which appeared to change from a geometric-series pattern to a log-normal pattern, and Mitchley's (1983) work on the seasonal variation in the relative abundance of chalkland perennials, apparently referred to contemporary processes. In other communities evolutionary processes may roughly be represented by a niche-apportionment model, but contemporary processes including stochastic variation could mask such a pattern. Although available data may not be sufficient to resolve this aspect in many communities, it is at least meaningful to acknowledge the importance of this issue. At the same time it should be noted that the processes of niche apportionment as embodied in models represent a highly idealized and simplified system which may never correspond exactly with reality. This being said, it is worth having models as a frame of reference which is simple enough to serve as a basis for comparisons. In this respect it may be argued that models should not be too realistic and complicated such that they lose generality. Although realism is a desired property of any model, the utility of a model needs to be balanced with its flexibility to describe a general pattern on varying spatio-temporal scales.

E. Species-oriented or Process-oriented Interpretation?

Another aspect of interpreting species abundance models which has received little attention concerns the status of species identity in niche apportionment (see Tokeshi, 1990a). This relates to the fact that models in general describe processes without specifying species identity. Thus, there are broadly two ways of linking niche apportionment with species identity: the species-oriented interpretation and the process-oriented interpretation. In the former, niches to be apportioned and ranked are assumed to be associated with the same ranking of species; the largest niche is always occupied by species *A*, the second largest by species *B*, the third by species *C*, and so on. Here, niche sizes of different species, together with the pattern of interaction among species, are considered to have been fixed through evolutionary time. In contrast, the process-oriented interpretation stipulates that niches of different size can be occupied by any species, i.e. species are neither tied to niche ranking nor to the order of niche invasion as envisaged in many niche-apportionment models. In this case what has been established through evolution is the processes of niche apportionment, i.e. how the total niche should be divided, wherein the identity of species is not important. In reality the situations in many communities are likely to be intermediate between these two extremes. Nevertheless, consideration of this aspect may reveal subtle differences between communities. This also relates to the distinction between equilibrium and non-equilibrium communities which has generated a considerable

amount of debate among ecologists (see Strong *et al.*, 1984). For example, the species-oriented interpretation of niche apportionment may be more relevant to communities which are relatively stable over a medium to long period of time, whereas the process-oriented interpretation may more often apply to non-equilibrium communities which undergo frequent changes in species abundance and composition. Amongst niche-oriented models, the random-assortment model typically relates to such non-equilibrium communities where the process-oriented interpretation is most appropriate.

On a relatively short time-scale (e.g. up to several generations of the organisms concerned), the abundance ranking of species in a community can be stable, even among communities which are thought to be subject to frequent disturbances. In such cases the species-oriented interpretation of species abundance models may be appropriate. On a longer, geological time-scale, however, virtually all communities undergo changes in species composition, and therefore the relevance of the species-oriented interpretation of models is likely to be reduced (e.g. Tsukada, 1972). On the other hand, this may not necessarily mean that the process-oriented interpretation instantly becomes more relevant. It is possible that successive communities through geological time are each approximated by a species-oriented pattern, while the process-oriented interpretation holds no relevance at all. Rather, the distinction between species- and process-oriented patterns may relate to more fundamental differences between communities, i.e. certain types of communities are more species-oriented while others are more process-oriented, irrespective of the time-scales involved.

F. Equilibrium versus Non-equilibrium Communities

In relation to the above discussion it is worth considering the problem of equilibrium versus non-equilibrium communities separately from the issue of species- versus process-oriented interpretation. Equilibrium communities are thought to be organized largely through biotic interactions (particularly interspecific competition), whereas various forms of physical disturbance and stochastic events dominate non-equilibrium communities. In the context of species abundance patterns, an interesting question is whether particular models can be associated with equilibrium or non-equilibrium communities. One confounding factor in this respect is that the definition of and the distinction between equilibrium and non-equilibrium communities is by no means clear, despite a commonplace use of these terms in the ecological literature.

In proposing three niche-oriented models (i.e. the broken-stick, the overlapping-niche and the particulate-niche models), MacArthur (1957) argued that these refer to equilibrium communities. However, the stochastic nature of niche apportionment as envisaged in these models may also allow them to

be interpreted as describing non-equilibrium communities. This confusion occurs because whether a community is in equilibrium or not may refer either to the absolute abundance values of different species (in which case those communities following stochastic niche-oriented models are mostly of a non-equilibrium nature) or to the relative competitive status of different species in a community (in which case niche-oriented models coupled with the species-oriented interpretation will relate to equilibrium communities). In other words, stochastic niche-oriented models can encompass both equilibrium and non-equilibrium characteristics, depending on different perspectives. If emphasis is placed on the essence of niche-apportionment models, i.e. a fixed total niche is divided amongst a group of species, an equilibrium-community view may apply. If, on the other hand, the aspect of stochasticity is stressed, a non-equilibrium view may predominate. Thus, the fit of these models cannot definitely be interpreted as indicating equilibrium versus non-equilibrium distinctions, with the exception of the random-assortment model which is most explicitly associated with non-equilibrium situations, as mentioned above.

Amongst statistically oriented models some workers consider the log-normal model as being related to stable, equilibrium communities (e.g. Whittaker, 1975; Gray, 1979, 1981; Stenseth, 1979; Preston, 1980), while others take the opposite view (Dennis and Patil, 1979; Hughes, 1984, 1985). Whilst there are semantic as well as some conceptual differences between the dichotomies of equilibrium/non-equilibrium versus disturbed/undisturbed communities, the argument that equilibrium or undisturbed communities are always described by the log-normal model may not have as strong a logical basis as has been thought. Heterogeneous assemblies of species where a multitude of factors operate quasi-randomly and independently of each other in a multiplicative manner can relate to both equilibrium/undisturbed and non-equilibrium/disturbed environments, the latter being dependent on the nature, magnitude and frequency of disturbance. At the same time it should be noted here that being in equilibrium does not necessarily imply total stasis in terms of species abundance. Rather, the spatio-temporal scale of investigation is likely to be an overriding factor influencing the fit of data to the log-normal model: a sufficiently large scale would guarantee a heterogeneous assemblage which necessarily demonstrates a log-normal pattern. This issue is discussed further in Section VIII.C in the context of its application to environmental assessment.

VII. PRACTICALITY OF MODEL TESTING

A. Fitting and Testing Models: Problems and Possibilities

One of the lingering problems of analysing species abundance patterns con-

cerns how models can and should be tested with real data. Here, obtaining parameter values of a model from a given data set should not be equated with testing the model's fit to the data concerned, because the former can be carried out without the guarantee of the latter. In contrast to the elucidation of mathematical properties of models including the estimation of parameters (e.g. Cohen, 1961; Bliss, 1965; Bulmer, 1974; Gauch and Chase, 1974; Kempton and Taylor, 1974; Pielou, 1975; Slocomb *et al.*, 1977), the practicality of model testing has received rather limited attention (Daget, 1976; Amanieu *et al.*, 1981). This section deals briefly with this aspect.

In empirical analyses of species abundance patterns, the most frequently used method of assessing the fit of a model to data is simple "visual inspection", which follows the calculation of parameter values and graphical representation of data. In fact, virtually all the proponents of different models have relied on visual inspection: Motomura (1932) for the geometric-series model; Preston (1948) for the log-normal model; MacArthur (1957) for the particulate-niche, the overlapping-niche and the broken-stick models, MacArthur (1960) and King (1964) for the broken-stick model; Williams (1964) for the log-series model; Frontier (1985) for the Zipf-Mandelbrot model; and Hughes (1986) for his dynamic model. It appears that this tradition of visual inspection is so deeply ingrained in this discipline that few people have seriously considered the deficiencies of such an approach. It is of course possible that visual inspection may be sufficient in some cases. An important point, however, is that visual inspection can so easily be influenced by subjective perspectives that it is difficult to expect logical objectivity which is the basis of scientific understanding. The conspicuous absence of statistical thinking on this particular matter contrasts sharply with the otherwise near-universal use of statistical tests to analyse patterns in community ecology.

Magurran (1988), following the pioneering work of Pielou (1975), advocates an extensive use of the χ^2 test of goodness of fit for comparing expected and observed patterns of species abundance. Although this test is widely used under various circumstances, its use with species abundance models which rely on the plotting of number of species against number of individuals per species (i.e. the log series, the log normal, the negative binomial, etc.) may require particular caution unless the total number of species involved is fairly large; if not, the test cannot reliably be applied. Thus, there is a serious dilemma in testing statistically oriented models; whilst large communities with well over 100 species, which may not represent an ecologically coherent entity, tend to allow a statistically rigorous testing of a species abundance model, relatively small (and hence more realistic) communities are not amenable to such a test. This practical difficulty of testing statistically oriented models further reduces their relevance in elucidating the organization of communities.

Another method for testing goodness of fit, which has rarely been used but may prove to be useful, is the Kolmogorov–Smirnov one-sample test. Like the χ^2 test, this test is concerned with the degree of agreement between the distribution of a set of sample values (e.g. observed abundances) and some specified theoretical distribution (see statistical references such as Siegel (1956)). One advantage of the Kolmogorov–Smirnov test is that it can be applied to very small samples, while the χ^2 test cannot. Furthermore, with relatively small samples which necessitate adjacent categories to be combined before χ^2 may properly be calculated, the Kolmogorov–Smirnov test is definitely more powerful than the χ^2 test (Siegel, 1956). Because ecological community data tend to be small in a statistical sense, there is constantly a risk of inappropriate use of the χ^2 test. Therefore, if choice is to be made between the χ^2 test and the Kolmogorov–Smirnov test, it is advisable to rely upon the latter in all cases.

Amanieu *et al.* (1981) have proposed the use of the Hellinger distance D^2 for a goodness-of-fit test in conjunction with principal-component analysis. D^2 is defined as,

$$D_{ab}^2 = \sum [\sqrt{P_a(i)} - \sqrt{P_b(i)}]^2$$

where $P_a(i)$ and $P_b(i)$ denote the proportional abundance of the i th rank in samples a and b (or observation versus theory), respectively. Amanieu *et al.* (1981) used this method to test the fit of the geometric-series, log-normal, MacArthur's broken-stick and Zipf–Mandelbrot models to marine benthic data. The statistical power of this method, however, is unknown and the null hypothesis is not well defined. In addition, application to MacArthur's broken-stick model is inappropriate (see below).

With regard to testing the stochastic niche-oriented models described in Section III.C, neither the Kolmogorov–Smirnov test nor the χ^2 test is suitable. This is due to the fact that the nature of "expected frequencies" to be compared with observed values is entirely different in these models. The point to be noted is that a single set of observed abundance values from a community is *not expected* to agree precisely with theoretical "expected" values of a stochastic model, because the latter values occur as an average of many replications. Where a single observation (one set of values) is concerned, a stochastic model cannot effectively produce expected values. Under these circumstances, the need to have replicated observations of abundance values becomes paramount for a meaningful comparison to be made between model and real data. Unfortunately, very few studies have paid serious attention to this aspect (Webb, 1974; Pielou, 1975; Tokeshi, 1990a).

In an attempt to resolve this problem of testing stochastic niche models, Tokeshi (1990a) adopted an entirely new approach that explicitly takes into account expected stochastic variation associated with a finite number of replications. The procedures are shown schematically in Fig. 18. On the

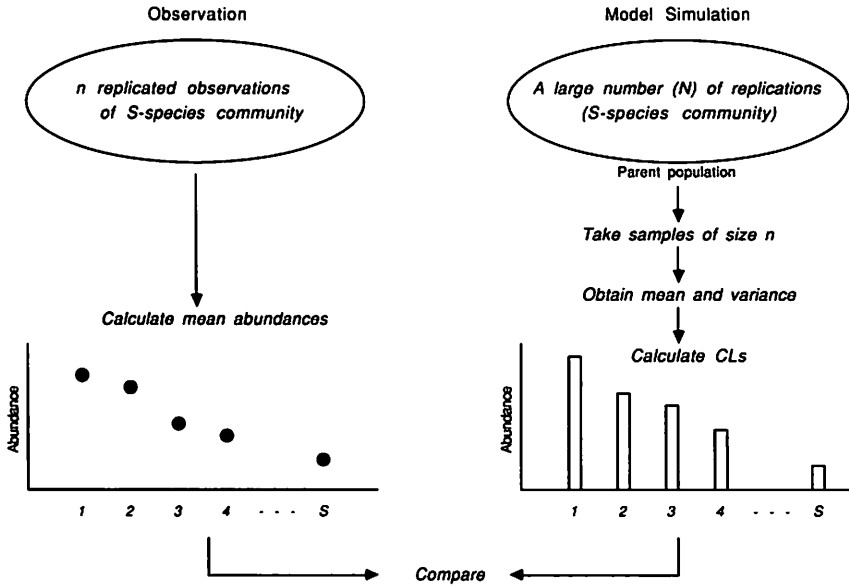


Fig. 18. Simulation method for testing the fit of a stochastic niche-oriented model with replicated observations. CL, Confidence limit.

one hand, $n (> 10)$ replicated observations (either spatially or temporally) are made on the species abundances of a community and mean abundance x_i is calculated for rank $i = 1$ (i.e. the most abundant species) to rank $i = S$ (the lowest abundance). On the other hand, for a given species abundance model a large number (N) of communities containing S species is constructed through simulation, from which the mean μ_i and variance σ_i of the abundance values for rank $i = 1$ to S are obtained. The next step is to compute the theoretical confidence limits of x_i , assuming that a sample of size n was repeatedly drawn from the parent population represented by N replicated communities of a single model. This is given as:

$$R(x_i) = \mu_i \pm r\sigma_i/\sqrt{n}$$

where $r = 1.96$ for a 95% confidence limit or $r = 1.65$ for a 90% confidence limit. These theoretical values can then be compared with the observed mean abundance values x_i . If all the values of x_i for $i = 1$ to S fall within the corresponding $R(x_i)$, the observed pattern of species abundance can be judged to be in conformity with the model's expectation.

In this case it is necessary to determine S , the "common" number of species in a community, according to replicated observations. If the total number of species does not vary from one observation to another, there will be no problem here. Frequently, however, this value varies and S will have to be adjusted to the minimum value among a set of replications.

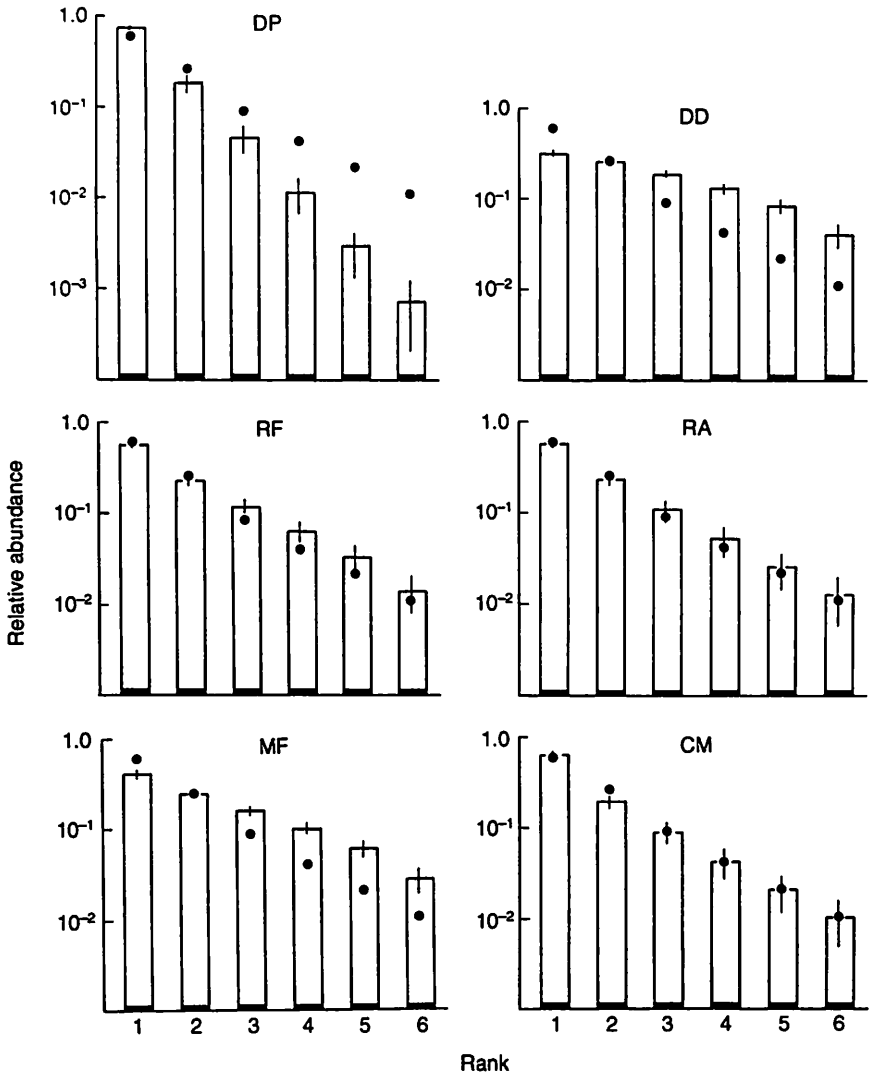


Fig. 19. Comparisons between observed values of relative abundance (biomass) in a chironomid community (●) and expected values from six models (histograms with 95% confidence limits). Models: DP, dominance pre-emption; RF, random fraction; MF, MacArthur fraction; DD, dominance decay; RA, random assortment; CM, composite. (Adapted from Tokeshi (1990a).)

This leads to a problem in that not all the species/ranks can be taken into consideration. Thus, it is important to confirm that either: (i) the total number of species does not show too drastic a variation among replicates; or (ii) S species account for a large majority (say 95%) of a community in terms of

abundance (number of individuals, biomass or cover) in replicate observations. In Tokeshi's (1990a) study of a freshwater chironomid community $S = 6$ was chosen since the six most abundant species accounted for at least 95% of the total chironomid abundance, in terms of both number of individuals and biomass, throughout the study period. In this analysis a total of 10 000 replicated communities (i.e. $N = 10\,000$), each consisting of six species, was created for each of six models, namely the dominance pre-emption, the random-fraction, the MacArthur fraction, the dominance-decay, the random-assortment and the composite models. Following this, theoretical 95% confidence limits for a mean of 26 replications (n) were computed for each of six ranks according to the formula given, and comparison was made between theoretical predictions and observed values (Fig. 19).

This method is applicable to the testing of stochastic niche-apportionment models in general, with explicit consideration of stochastic variation in real data. It is worth noting that, depending on whether species-oriented or process-oriented interpretation is adopted (see Section VI.E), observed mean abundances may be calculated in different manners. One possible disadvantage of this method relates to the time-consuming nature of simulation, especially for large S ; this, however, should not prove prohibitive with the wide availability of computers. Obviously, it is important to have large N so that the parent population of S -species communities is not biased (as is expected in any Monte Carlo type simulation).

In summary, the Kolmogorov–Smirnov one-sample test is probably the most suitable for testing the fit of deterministic species abundance models, whereas Tokeshi's simulation method is so far the only test available that is applicable with reasonable rigour to stochastic species abundance models.

B. Importance of Replicated Observations

As is implied in the previous section on testing models, the importance of replicated observations cannot be overemphasized, especially in relation to stochastic models. The point is that these models are untestable with unreplicated data. Some investigators who closely examined MacArthur's broken-stick model clearly realized this (e.g. Webb, 1974; Pielou, 1975), but their message failed to engage the serious attention of those applying the model to real data. This unfortunate state of affairs is due partly to the fact that no alternative method which incorporates replicated observations and is capable of coping with stochasticity has been proposed to replace the age-old tradition of visual comparison of unreplicated data with theoretical expectations. With the recent development of methodology as mentioned above, however, the practice of taking replicated data should be firmly established, which would certainly lead to an increased level of information and understanding.

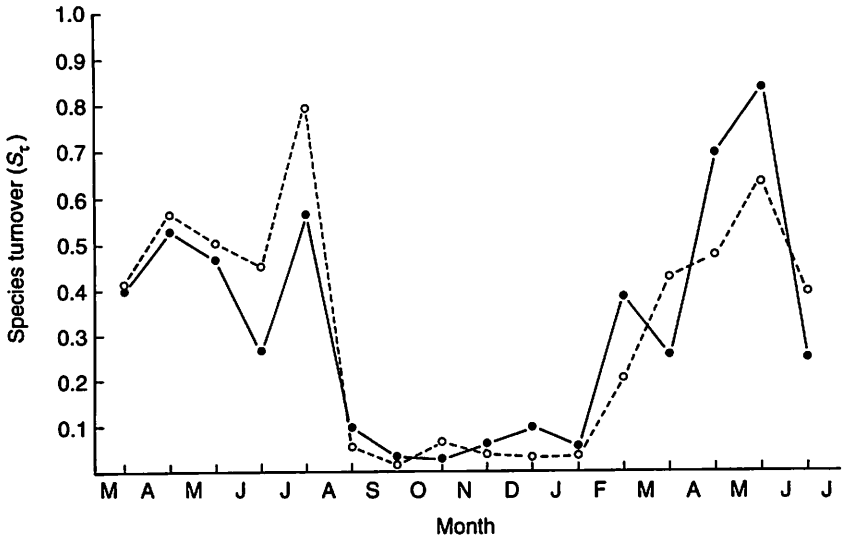


Fig. 20. Temporal variation in species turnover (S_{τ}) in a chironomid community. Calculations based on number of individuals (\circ) and biomass (\bullet). (After Tokeshi (1990a).)

In this respect one aspect which is worth considering relates to the nature of replications. In theory, replications need to be mutually independent, implying that communities which are spatio-temporally distinct should be observed. On the other hand, what is under investigation in this context is a particular community and its community-specific pattern of species abundance, rather than global patterns (see Section VI.C). Thus, there is a logical dilemma in obtaining replicated observations for testing community-specific patterns based on stochastic niche-apportionment models; we require independent replications of a single community, which is essentially a contradiction in terms. There is no easy solution to this and it is necessary to adopt a case-by-case approach for different communities under different circumstances. For example, Tokeshi (1990a) assessed species turnover S_{τ} which measures the change in species composition from one replicate to another (on either temporal or spatial scale), thus:

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

where $P_i(t)$ and $P_i(t+1)$ denote proportional abundance of species i in sample t and $t+1$, respectively. Samples taken in spring and summer demonstrated high species turnover (Fig. 20), so these were treated as one entity representing reasonably independent, heterogeneous replications, in contrast to another entity (autumn-winter) which was strongly dependent and

homogeneous internally. Obviously, the former entity represents more appropriate replications. This allowed a more careful analysis of species abundance patterns in a chironomid community than would otherwise have been the case.

Replicated observations would have slightly different meanings in statistically oriented models, which essentially assume a deterministic character. An attempt explicitly to compare replicated data with statistically oriented models is virtually non-existent, due perhaps to the fact that these models are designed to be applied to a single large sample. Nevertheless, it will be highly interesting to examine the variation in parameter values of a single community, using replicated observations which are collected with the same degree of care as is desirable with stochastic models. Such detailed analyses would lead to a better understanding of species abundance patterns in communities.

C. Resolution/Discriminant Power of Models

Whilst different models describe different processes of species abundance, there is always a concern as to how easily different models or patterns can be distinguished from each other. Apart from the characteristics of models there are two factors which will influence the discriminatory power of models: (i) the total number of species S ; and (ii) the total number of individuals N . As either S or N decreases in value (in reality these two are often closely associated and, therefore, change in concert), distinguishing between different models becomes more difficult. One way out of this difficulty is to increase the overall sample size. However, "smallness" may be an important characteristic of the community concerned, and in this case artificially increasing the sample size to augment S and N will destroy the community's identity. This problem is particularly relevant to fitting the log-series and the log-normal models to data. Taylor (1978) demonstrated that both the log-series and the log-normal models adequately fit a sample of moths from a single site, but only the log-normal model fits the amalgamated data covering 225 sites in Britain. A similar situation occurred with samples of fish from the Arabian Sea (Magurran, 1988). Thus, these two models are generally indistinguishable with respect to small communities (see Routledge, 1980), and only through redefining communities and their boundaries will it become possible to distinguish them. This relationship can be represented schematically (Fig. 21), including the geometric-series model which was originally proposed as a statistical model (Motomura, 1932) and is recognized to encompass fundamentally the same principle as the log-series model (May, 1975). These three models may be considered to encompass the same system, the only major difference being the size of assemblage considered or the scale of investigation. Whilst the log-normal model refers to an entire (heterogeneous) assemblage, the log-series one represents a part of it, with a conse-

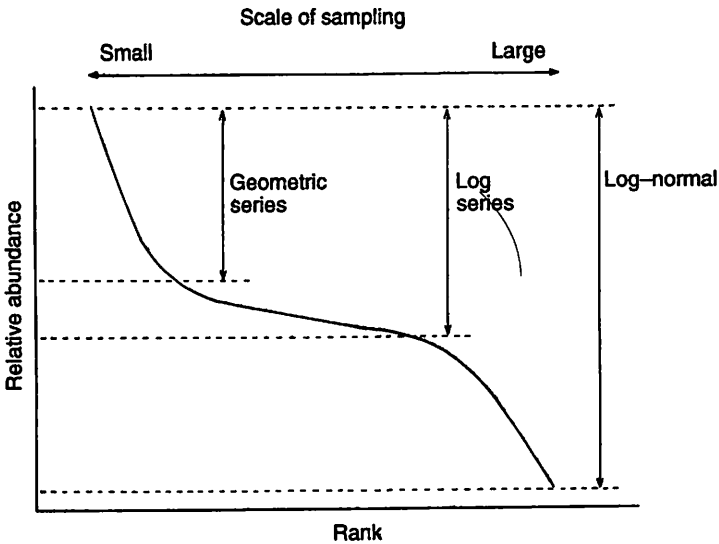


Fig. 21. Nested relationship between the geometric-series, the log-series and the log-normal patterns based on the scale of sampling.

quence that medium-sized assemblages can be described by both the log-normal and the log-series models, as mentioned above. Even smaller communities are approximated by the geometric-series model and it is also theoretically conceivable to fit the other two models to such data (though few researchers will be tempted to do so). Where a set of models inherently possesses a nested relationship like this, distinguishing different patterns (models) is directly influenced by how community boundaries are defined. It should be noted that this is not a trivial matter in the analyses of species abundance patterns; the debate about whether the log-normal model successfully fits a variety of ecological data or not may largely be a matter of scale, rather than anything profoundly biological.

Despite structural similarities of niche-apportionment models which have recently been introduced, discriminant powers of these models appear reasonably good, as was demonstrated for 15-species communities (Fig. 1(b)) and six-species communities (Fig. 19). In the latter example, only the random-assortment model fitted the field abundance data expressed as biomass, whereas the random-assortment and the random-fraction models both fitted the numerical (i.e. number of individuals) data (see Tokeshi, 1990a). In testing these models, the resolution (i.e. how narrowly abundance values can be predicted) critically depends on the number of replicated observations made, through the simulation method described in the previous section. Apparently, the expected confidence limits expand and the model resolution drops as a smaller number of replications is taken. Conversely,

a larger number of replications will lead to a clearer separation of potentially similar patterns. This constitutes a major reason why adequate replications are important in guaranteeing analytical rigour in this field.

VIII. ALLIED ASPECTS

A. Links with Diversity Indices

Species abundance models have generally been considered hand in hand with diversity indices, mainly because they share the same objective of describing communities based on similar kinds of information. The main difference between species abundance models and diversity indices is that the latter attempt to summarize in a single numerical value how diverse a community is, whereas the former avoid such condensation of information and focus instead on the overall pattern of diversity represented by a set of abundance values. While in theory it is more desirable to make full use of available data in the form of species abundance patterns (see Southwood, 1978), there are numerous occasions where a single "catch-all" expression of a diversity index is more practical and appealing to the recipients of the information, whether researchers, conservationists or managers of wildlife resources.

Various diversity indices proposed to date are listed in Table 2, with an indication of each model's inclination towards either species richness or evenness, the two elements of diversity. Many of these indices have repeatedly been dealt with in reviews (Peet, 1974; Pielou, 1975; May, 1975; Grassle *et al.*, 1979; Magurran, 1988) and, therefore, references should be made to these. Hill (1973) considered a unifying relationship among indices, and Magurran (1988) made an extensive comparison of different indices using field data. Amongst indices, only k of the geometric series, α of the log series and λ of the log-normal methods are directly linked to a species abundance model, while the Q statistic is derived from cumulative ranked frequencies. The log-series index α has in particular been strongly recommended as a satisfactory measure, because it is not unduly affected by sample size and possesses a good discriminant ability (Taylor, 1978). Taylor considers that the index is useful even where the log-series model does not fit the data concerned. This logic of somewhat divorcing a diversity measure from an underlying species abundance model may also be applied to the index k of the geometric-series model, as originally intended by Motomura (1932); the slope k on the rank-abundance graph expresses something about the complexity of an assemblage, irrespective of a fit between data and the model (see Section IV.C). However, in view of the fact that the geometric-series model appears to cover a smaller range of communities than the log-series model (see the previous section and Fig. 20), α may be a more suitable index than k . On the other hand, diversity of small (and perhaps ecologically more

Table 2
Indices of diversity

Index	Formula	Emphasis of index	References
Species richness	S	Richness	
Standardized S (rarefaction)	$S_n = \sum [1 - \binom{N-n}{n} / \binom{N}{n}]$	Richness	Sanders (1968); Hurlbert (1971)
Log series α	$N = \alpha \ln(1 + N/\alpha)$	Richness	Fisher <i>et al.</i> (1943)
Log-normal λ	S^*/σ	Richness	Pielou (1975)
Q statistic	$\frac{(0.5S_{25} + \sum S_i + 0.5S_{75})}{\log(N_{25}/N_{75})}$	Richness	Kempton and Taylor (1976, 1978)
Odum <i>et al.</i>	$S/\log N$	Richness	Odum <i>et al.</i> (1960)
Margalef	$(S-1)/\log N$	Richness	Margalef (1968)
Simpson, $d (= \sum p_i^2)$	$1/d$	Richness	Simpson (1949)
	$1 - d$	Evenness	Hill (1973), Peet (1974), DeJong (1975)
	$1 - \sqrt{d}$	Evenness	Hill (1973), Peet (1974), DeJong (1975)
McIntosh, D	$(N - U)/(N - \sqrt{N})$	Evenness	McIntosh (1967)
McIntosh, E	$(N - U)/(N - N/\sqrt{S})$	Evenness	Pielou (1969)
Shannon-Wiener, H'	$-\sum p_i \ln p_i$	Evenness	Pielou (1969)
Shannon-Wiener, J'	$H'/H'_{max} = H'/\ln S$	Evenness	Pielou (1969)
Brillouin diversity, H_b	$(\ln N! - \sum \ln N_i!)/N$	Evenness	Pielou (1969)
Brillouin evenness, J_b	H_b/H_{bmax}	Evenness	Pielou (1969)
Berger-Parker, d	N_{max}/N	Evenness	Berger and Parker (1970), May (1975)

N , total number of individuals; N_i , number of individuals belonging to species i ; p_i , proportion of species i among total individuals ($= N_i/N$); n , standardized sample size; S^* , estimated total number of species (log-normal model); σ , log-normal standard deviation; S_{25} , S_{75} , number of species in the 25% and 75% quartiles, respectively; N_{25} , N_{75} , number of individuals in the 25% and 75% quartiles, respectively; $U = \sqrt{\sum N_i^2}$; N_{max} , number of individuals belonging to the most abundant species.

realistic) communities could be more conveniently expressed by k than by α , or equally adequately by both. In this respect it may be worthwhile to note that these two indices tend to stress different components of diversity; α for species richness and k for evenness. Comparison of these two indices as applied to small communities remains a further subject of study.

Much effort has been directed towards selecting the diversity index which works best with real data. For this it is necessary to establish a set of criteria to assess merits and demerits of indices, but this is not as straightforward as it might appear. For example, May (1975) lucidly demonstrated that the Shannon index H' is a poor discriminator of assemblages with underlying patterns of the log-series, the log-normal and the broken-stick models. However, it is an entirely different matter whether discriminating between these patterns is a trait crucially required of a diversity index; it is possible to argue (for the sake of argument) that such separation, if needed, can be achieved by a more straightforward analysis of species abundance data, while diversity indices should be assigned to other tasks. A number of criteria which are worth taking into account include:

- (i) susceptibility to sample size;
- (ii) ease of calculation;
- (iii) ease of interpretation;
- (iv) to which of the two elements of diversity, species richness or evenness, more importance is to be attached;
- (v) discriminant power;
- (vi) to what type of organisms more importance is to be attached, i.e. common, intermediate or rare species;
- (vii) applicability to relatively small or large data sets; and
- (viii) generality of use in past and present works.

Obviously the relative importance of these criteria may vary from one study to another and there cannot be a universal "best buy" in this matter, as no index can cover every aspect maximally. Thus the choice of a diversity index is always a compromise between several of the criteria listed above.

B. Species–Area Relationships

The observation that the number of species belonging to a particular taxonomic group tends to increase with increasing area (referring in particular to islands and other analogous habitats of patchy spatial occurrence) has received substantial attention (e.g. Preston, 1960, 1962; Williams, 1964; MacArthur and Wilson, 1967; Simberloff, 1972). Arrhenius (1921, 1923a,b) considered a curvilinear relationship between the number

of plant species (S) and area (A), which can be described as a power function

$$S = cA^z$$

where c and z are constants. When transformed logarithmically,

$$\ln S = \text{Constant} + z \ln A \quad (1)$$

Another description of species–area relationship was proposed by Gleason (1922, 1925) who considered an exponential form to be more appropriate, thus,

$$S = \text{Constant} + z \ln A \quad (2)$$

While Fisher *et al.* (1943) and Williams (1943, 1944, 1947) have demonstrated that eqn (2) directly results from the log-series distribution of species abundances combined with the assumption that population size scales linearly with habitat area, Preston (1962) and MacArthur and Wilson (1967) have shown that the canonical log-normal distribution with the same assumption leads to eqn (1). Subsequently, the view that the canonical log-normal model and the power function for the species–area relationships are widely applicable has come to be accepted (see Connor and McCoy, 1979; Sugihara, 1981). May (1975) has shown that the general log-normal model with the parameter γ ranging between 0.6 and 1.7 produces species–area curves which are in rough agreement with data, though these relationships are not exactly linear regressions of $\ln S$ on $\ln A$; nevertheless, eqn (1) is adequate as an approximate rule. It should be stressed that a fit of the power or exponential function to species–area data does not necessarily imply that the assemblage has an underlying log-normal or log-series pattern of species abundance; there is as yet no proof of one-to-one correspondence in this matter. As Connor and McCoy (1979) pointed out, species abundance patterns need to be determined empirically in their own right.

Much interest has centred around the value of z , the slope of the $\ln S$ versus $\ln A$ regression. Because the exact relationship between $\ln S$ and $\ln A$ is not a linear one when the canonical log-normal distribution is assumed, fitting a linear regression to theoretical expectations leads to a slight overestimation (e.g. $z = 0.262$ in Preston (1962), and $z = 0.263$ in MacArthur and Wilson (1967)) compared with the asymptotically exact value of 0.25 (May, 1975). Observed values often fall in the range 0.2–0.4 (Preston, 1962; MacArthur and Wilson, 1967; May, 1975; Schoener, 1976), which led Connor and McCoy (1979) to suggest mathematical artefacts as a reason, which in turn was disputed by Sugihara (1981). It is still doubtful whether much biological insight can be gained from the postulated tight clustering of data points around the theoretical $\ln S$ versus $\ln A$ regression expected from the canoni-

cal hypothesis ($\gamma = 1$). In this respect it will be worthwhile to consider two optional hypotheses: (i) constancy in z has a biological meaning because it is closely linked to the canonical log-normal distribution (which has a biological meaning); and (ii) constancy in z has a biological meaning irrespective of the superficial resemblance to the expectations of the canonical log-normal distribution (which has little biological meaning). Moreover, it may still be premature to conclude the constancy in z in the first place. Thus, broadly, two questions need to be resolved: (i) whether or not constant z is a reality among ecological communities; and (ii) if yes, whether it has a non-trivial, biological meaning.

Setting aside the issue of constant z , there is no doubt that the general species–area relationship which is most conveniently described as a power function (eqn (1)) exists in nature, as has been attested in a large body of literature (e.g. Preston, 1962; MacArthur and Wilson, 1967; Schoener, 1976; Lawton and MacGarvin, 1986; Claridge, 1987). On the other hand, mechanisms leading to such a relationship are at best obscure and must include: (i) habitat heterogeneity—a larger area encompasses more diverse microhabitats which support more species; (ii) susceptibility to extinction—a larger area allows a larger population size, leading to a reduced chance of local extinction; and (iii) susceptibility to immigration—a larger area receives more immigrants from source pools. Although Connor and McCoy (1979) proposed what they called “passive sampling” (i.e. larger area collecting more species as a purely sampling process) as a mechanism devoid of biological processes, this argument cannot logically be established as being separate from the process of immigration, which is most profoundly biological. It then follows that the argument that a species–area relationship derived from such passive sampling should be used as a null model of testing biological interactions (Connor and McCoy, 1979) is without foundation. There have been very few studies which have examined these aspects in conjunction with the analyses of species–area relationships. It is most likely that, rather than operating singly, these mechanisms are simultaneously involved in community organization with their relative strength varying among communities and under different environmental conditions.

Despite Connor and McCoy's (1979) thorough examination, no biologically significant global pattern has emerged regarding the values of z in ecological communities, apart from an inverse relationship between the linear correlation coefficient of z and latitude. This may be due to under-reporting of data, particularly those which do not appear to fall within the conventional mould. Perhaps the fact that the analysis of species–area relationships explicitly takes into account the effects of varying spatial scales should be considered as an important advantage over one-scale measures such as diversity indices in characterizing communities and, therefore, should encourage more research involving it.

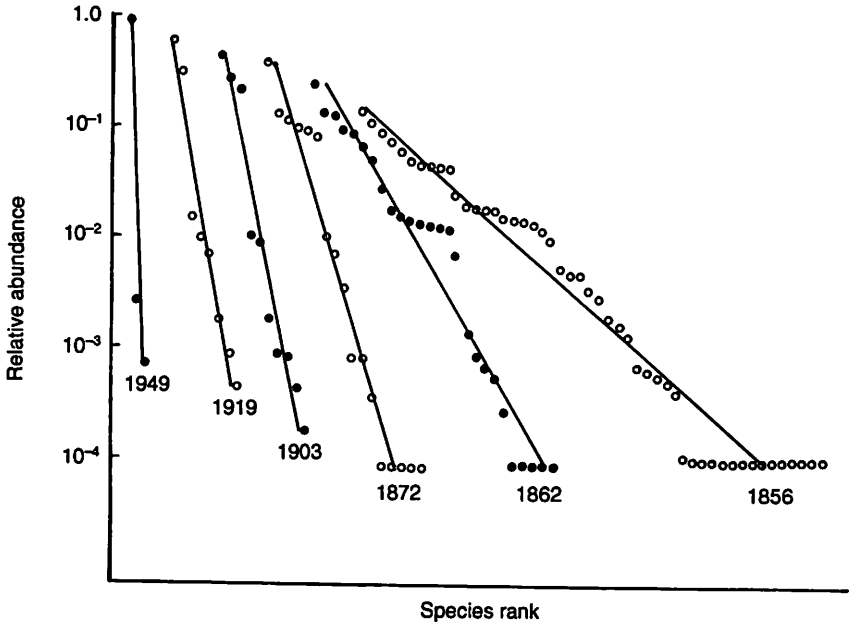


Fig. 22. Change in the relative abundance pattern of plant species in an experimental grassland subjected to continuous application of nitrogen fertilizer since 1856. (Data from Brenchley (1958).)

C. Application to Environmental Assessment

While analysis of species abundance patterns can in theory be done with any community, its application in the context of environmental assessment is meaningful only when it is known *a priori* that discernible changes in species abundance pattern are associated with some kind of environmental degradation. In other words, patterns expected of a natural, undisturbed community must first be recognized, which would undergo changes under environmental modification of human origin such as organic pollution.

May (1981) observed that the log-normal pattern which is often associated with undisturbed communities tends to be replaced by the geometric-series or log-series pattern as organic pollution progresses. This has been demonstrated by data on diatom communities (Patrick, 1963, 1968, 1973; Patrick *et al.*, 1954) and a grassland community subjected to a continuous heavy application of nitrogen fertilizer (Brenchley, 1958; Williams, 1978; Kempton, 1979). If the focus of attention is the change in dominance/evenness relationships following environmental degradation, however, uniform application of the geometric-series model to an entire data set is a more straightforward approach, with the slope k being interpreted as an index of dominance/evenness (see Section IV.C). This is illustrated in Fig. 22 where

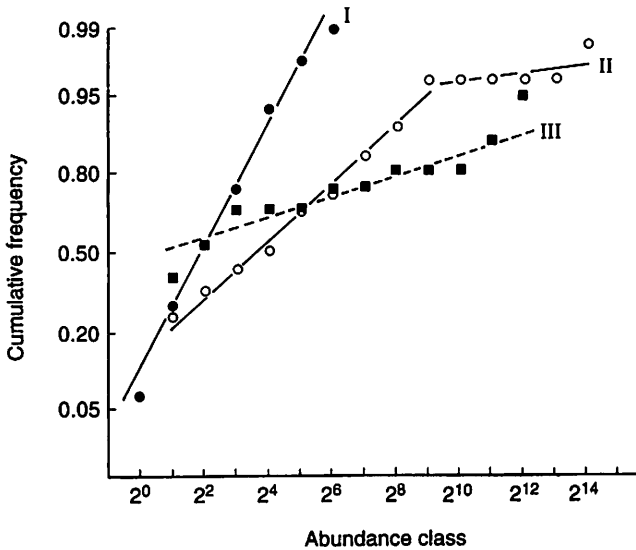


Fig. 23. Temporal changes in the pattern of the cumulative frequency of species (probability scale) plotted against logarithmic abundance classes for marine benthic communities subjected to organic pollution. Pollution started in 1966. I, 1963; II, 1970; III, 1973. (Data from Pearson (1975).)

the geometric-series model was fitted to changing patterns of relative abundance of a grassland community mentioned above. It is obvious that dominance steadily increased and species richness decreased as the effects of environmental stress accumulated over a century.

Gray and his colleagues (Gray, 1979, 1981; Gray and Mirza, 1979; Gray and Pearson, 1982) proposed that undisturbed, equilibrium communities are described by the log-normal model and that departure from the log-normal distribution can therefore be used as a criterion for detecting organic pollution. Gray and Mirza (1979), analysing marine benthic data, plotted geometric classes of abundance (number of individuals per species) on the abscissa and the cumulative percentage of species (probability scale) on the ordinate (Fig. 23). On this graph a single straight line indicative of a log-normal pattern (see Bliss, 1965) fits an undisturbed community (Fig. 23, line I), while pollution induces the upper part of a line to assume a shallower slope, thus resulting in a combination of two lines (Fig. 23, line II) (but see a counterargument by Shaw *et al.* (1983)). Gray and Mirza (1979) postulated that this is because some species (of medium to high abundance) become more abundant while rare species do not change in abundance under mild pollution stress. Even heavier pollution produced a straight line (Fig. 23, line III), but with shallower slope and covering a wider range of abundance classes, implying a larger variation in abundance among species.

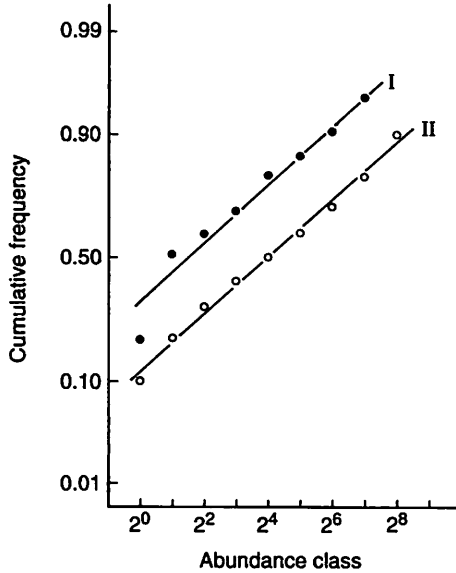


Fig. 24. Comparison between a 41-species community following a log-normal pattern (I, data from Gray and Mirza (1979)) and a hypothetical 10-species community (II) following a geometric series (abundance represented by 2^x individuals each).

As has been stressed by Gray (1983) in response to Shaw *et al.* (1983), there seems to exist little room for disputing the fact that the log-normal model is generally applicable to large heterogeneous assemblages such as samples of marine benthos from a relatively large area, since the log-normal distribution represents what is statistically expected from large numbers. On the other hand, the plotting method used by Gray and Mirza (1979) is insensitive to different patterns of species abundance, thus casting some doubt upon its utility to detect supposed departure from a log-normal pattern. First, the cumulative probit plotting greatly facilitates the fit of a linear regression because it typically emphasizes the gradually increasing middle range, whilst conveniently excluding the highest cumulative point (100%). This means that species belonging to the highest abundance class are always ignored. Second, this plotting is quite insensitive to changes in species richness, in particular. For example, in Fig. 24 line I is fitted to Gray and Mirza's (1979) data on station A of the Oslofjord representing a total of 41 species under undisturbed conditions, while line II is fitted to a hypothetical community of 10 species following the geometric-series model (see figure legend) which is considered to represent, as mentioned earlier, a somewhat disturbed situation (see May, 1981). Note that a supposedly impoverished community has an equally good, or slightly better, linear-regression fit compared with the undisturbed benthic community. Furthermore, contrary to Gray and Mirza's

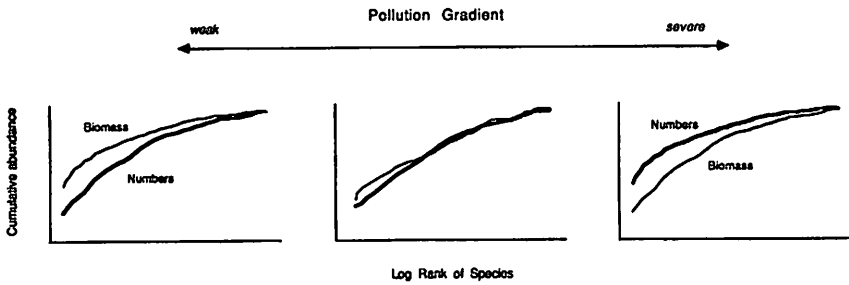


Fig. 25. Hypothetical patterns of percentage cumulative abundance in terms of number of individuals and biomass plotted against log (species' rank) along a pollution gradient. (Adapted from Warwick (1986).)

(1979) proposition that disturbed communities have a shallow slope, the slopes of these two apparently different communities are not noticeably different on this graph, nor are the ranges of abundance values covered. Thus the sensitivity of the proposed plotting method to different patterns is questionable on theoretical grounds, making it unlikely that the method is universally applicable for detecting departures from a log-normal pattern; at best, only certain types of departure can be discerned. This implies that comparisons on a spatial scale, i.e. interhabitat comparisons, cannot reliably be made using this method. Indeed, Gray and his colleagues have somewhat gone away from this method to use multivariate-type analyses for assessing pollution effects (Gray *et al.*, 1990).

Another method for detecting organic pollution was proposed by Warwick (1986), with respect to marine macrobenthic communities of the soft sediment. He used the cumulative abundance graph (see Section IV.E) with the log(rank) of species to plot two curves, the one based on biomass and the other on numbers of individuals (Fig. 25). Warwick hypothesized that unpolluted situations would show the biomass curve to be positioned above the numbers curve, while a moderate level of pollution would lead to the two curves more or less overlapping. Yet a grossly polluted situation would lead to the inverse of unpolluted situations, with the numbers curve being above the biomass curve. Warwick (1986) suggested that the transition from an unpolluted to a moderately polluted situation corresponds to the disappearance of large species which are dominant in terms of biomass but not in numbers under the unpolluted situation, and the transition from a moderate to a heavily polluted situation corresponds to the increase in number of small, pollution-tolerant species (such as oligochaetes and some polychaetes) which are not dominant in terms of biomass.

Apart from the need to collect more data to bear on this hypothesis, there are a number of important issues which require clarification. First, what is hypothesized here as the unpolluted situation (i.e. the biomass curve being

above the numbers curve on the cumulative abundance plot) is simply another expression of "biomass being less equitably distributed than numbers among species in a community" (see Section V.D), the pattern that is universal and not peculiar to marine macrobenthic communities. Thus, departure from this situation needs to be considered and framed on a wider theoretical basis, not restricted by the particular ecology of marine macrobenthos. If numerically non-dominant but large-bodied species are responsible for the change in Fig. 25, it would be all the more straightforward to designate these as "indicator species" and monitor changes in their abundance for detecting pollution, rather than relying on somewhat indirect information in the shape of cumulative abundance plotting. Indeed, note that the relative positioning of the two curves on this graph will in all practicality be determined by the first two or three points (species). Secondly, for the method to be claimed sensitive it is necessary to demonstrate that communities under organically polluted conditions do not show the "biomass above numbers" pattern (i.e. biomass being less equitably distributed than numbers), with more rigorous theoretical reasoning than has been proposed. This point is of both practical and theoretical importance, since there is as yet no concrete theoretical basis on which to argue for more equitable distribution of biomass than numbers (see Section V.D). The very fact that a limited number of samples from polluted areas did show this pattern (e.g. Warwick *et al.*, 1987) is highly interesting and merits further analysis. Thirdly, even if the method is to be confined to the limited domain of marine macrobenthic communities, it is important to define the community boundaries in a more rigorous, standardized manner. For example, the determination of the numerical abundances of small infaunal organisms ("very small" meiofauna are apparently excluded from Warwick's (1986) consideration) is greatly affected by the mesh size chosen, which would in turn crucially affect the eventual comparison of two curves on the graph. *Ad hoc* inclusion or exclusion of organisms of different sizes would reduce the objectivity of the analysis.

In the general context of environmental assessment an important question remains as to whether a certain type of disturbance such as organic pollution can always be expected to induce a pattern of change which is detectable by one or another method. At the same time, the degree of disturbance which is needed to cause such a detectable change must be known. If a method is capable of detecting only a major disturbance, its utility will naturally be limited. In a more philosophical vein, what is implied by pollution "effects" needs to be better defined; otherwise, those recognizable by a particular method can only be regarded as "effects", creating a somewhat circular argument. It seems, therefore, that a host of issues needs to be resolved and improvements be considered before any method is accepted as a general technique for assessing the impact of organic pollution.

On a wider perspective, the contention that equilibrium communities are

represented by the log-normal model requires further investigations (see Section V.E). One problem in this matter is that because the log-normal model applies only to large, heterogeneous assemblages, small communities with a relatively small number of species, which tend to form ecologically more realistic entities, cannot logically be incorporated into this scheme; it is obviously unreasonable to assume that large communities are mostly at equilibrium, while small communities are not. Note that the difference in opinion between Shaw *et al.* (1983) and Gray (1983) is partly due to different perceptions of the definition of "community" and "sample" (see Sections IV.A and IV.B), thus inadvertently pointing to the importance of this issue. Similarly, the link between disturbed communities and the geometric-series or the log-series model (Stenseth, 1979) may not be as straightforward as has previously been suggested. Therefore the general problem of one-to-one correspondence between model and pattern also needs to be considered within the framework of environmental assessment.

IX. CONCLUDING REMARKS

A. Towards Integrated Research on Community Structure

Having reviewed the current status of research on species abundance patterns, there are a number of points worth emphasizing for the future development of this discipline.

First of all, more attention needs to be paid to the spatial and temporal variation in species abundance patterns for a given community. The importance of making replicated observations cannot be overstressed in this respect, since variability is the gist of natural populations and communities. At the same time it is worth considering patterns on different spatio-temporal scales, a theme which is applicable not only to the study of species abundance patterns but also to any pattern of community organization.

Traditionally, there has been a tendency to deal more with relatively large communities than with small ones when analysing species abundance patterns, partly because of the popularity of the log-series and the log-normal models. On the other hand, experimental and observational studies of community organization focusing on biotic and abiotic factors tend to deal with small communities which form ecologically more closely knit entities. Thus there is a clear need for more small communities to be analysed for species abundance patterns, particularly with reference to niche-oriented models. In this context it may also be worth exploring the relevance of statistically oriented models to small communities, including the practical aspect of fitting them to such data.

In relation to the analysis of species abundance patterns in small com-

munities of ecologically closely related species, an aspect which has not been sufficiently appreciated is the importance of combining different approaches to the elucidation of community organization. In broad perspective, species abundance patterns represent just one facet of community structure, whilst there are other facets to be considered. Thus a better understanding of community organization can be achieved by analysing various facets of a single community through the combination of observational, experimental and analytical approaches. The fact is, none of the methods can be decisive enough on its own to make a categorical statement about community structure; for example, field experiments are widely acknowledged as a powerful tool for unravelling community structure, but can generally cover only a limited range of temporal and spatial scales and thus could give a somewhat biased picture. Under these circumstances the best that can be achieved is to obtain a maximum degree of confidence in making inferences, with supporting evidence derived from various analyses. Research on a freshwater chironomid community (Tokeshi, 1986a,b, 1990a,b, 1992, 1993; Tokeshi and Townsend, 1987) that integrates analyses of resource utilization, colonization experiments, body-size relationships, diversity, and species abundance patterns represents an attempt in this direction.

Species abundance patterns are undoubtedly based on evolutionary as well as contemporary processes. Because of this intermeshing of long- and short-term processes, the elucidation of precise mechanisms leading to a particular species abundance pattern is not easy. It is obvious that a fit to a particular model alone should not immediately be linked to an assertion that specific processes envisaged in the model are in reality governing the natural system concerned. On the other hand, this does not in turn necessarily justify an argument that models should always be used as statistical descriptions and nothing more. By applying not only one but a number of species abundance models (see Tokeshi, 1990a) and synthetically combining other approaches, whether experimental, observational or analytical, it is possible to enhance confidence in inferences made, or alternatively cast doubt on them. Such a multi-faceted investigation of community structure is clearly needed, and models of species abundance patterns are useful in the sense that they suggest possibilities to be considered. Judicious and critical use of the analysis of species abundance patterns, rather than branding it as form of statistical exercise and relegating it to description only, is perhaps the best approach to enhancing our understanding of ecological communities.

Last but not least, there is a need for gathering species abundance data on a variety of communities covering a wider range of species than has so far been the case, in order to perform more comparative analyses. In this context it is worth paying more attention to the relevance of phylogenetic grouping and evolutionary history in species abundance patterns. The question of global versus community-specific patterns can fruitfully be resolved only

through comparative analyses of patterns in a diversity of communities. In this respect it can be argued that the study on species abundance patterns beyond model descriptions has begun only recently.

ACKNOWLEDGEMENTS

Thanks are due to Drs D. Jewson, D. Griffiths and J. Zlinszky, Prof. Wood and other members of the Freshwater Institute, University of Ulster, for various forms of logistical support during the preparation of this work, and to Dr J. Gray, University of Oslo for commenting on the manuscript.

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