Power fraction: a new explanation of relative abundance patterns in species-rich assemblages

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Analysis of species abundance patterns in assemblages with relatively large number of species has been an important issue in community ecology for several decades. Following Preston's pioneering work, Sugihara proposed a model to account for such patterns in a diverse range of communities, which has been given further support from analyses of recent data that are considered to be of particularly high quality. This paper re-examines Sugihara's approach and points out that there has been confusion and misunderstanding among workers as to the exact nature of his widely-publicised hypothesis. In particular, the 'fixed ratio' division cannot be considered as an expected (average) pattern of the triangular assumption; they represent fundamentally different entities. Further, Tokeshi's Random fraction model should not be treated as synonymous with Sugihara's fixed division model. The RF model has its own identity as a niche apportionment model and can account for patterns in some species-rich assemblages. With this background, this paper proposes a new niche apportionment model to explain relative abundance patterns in ecological communities, termed the Power fraction model. The PF model envisages that the probability (p) of selection for a subsequent division is positively but weakly related to niche sizes/abundances (x) of species as a power function ($p \propto x^k$ where $0 \leq k \leq 1.0$; i.e. niche division/invasion is more likely in species with high abundance/large niche) and that division occurs with any ratio (i.e. a barrier to split a species' population may occur anywhere in the species' range), with the RF model representing an extreme case on the spectrum of the PF model. The Power fraction model with $k \sim 0.05$ or $k \sim 0-0.2$ demonstrates a good fit to a miscellany of data from species-rich assemblages. The PF model is not restrictive in terms of division ratios, and can be framed as either a community-specific or a global explanation of patterns. Thus, the new model is more flexible and realistic from ecological and evolutionary points of view and offers a possibility of cross-community comparisons within a uniform, integrative framework.

Pattern of relative abundances of species is a major issue in community ecology (MacArthur 1960, May 1975, Pielou 1975, Gray 1987, Magurran 1988, Tokeshi 1993). Over the years, ecological data collection of local faunas and floras led to a search for ways of describing and interpreting the patterns of relative abundances of different species in those assemblages (e.g. Motomura 1932, Fisher et al. 1943, Preston 1962a, b). In addition to such historical trends, in recent years an increasing importance has been attached to the analysis of assemblages with relatively large numbers of species, as the problems of global biodiversity draw attention from ecologists working on different taxa and ecosystems (e.g. Wilson and Peter 1988). Patterns of relative abundances of species in such assemblages have generally been considered with reference to statistically oriented models such as the log series and the lognormal model (Fisher et al. 1943, Preston 1962a, b; see reviews in May 1975 and Tokeshi 1993). In particular, Preston (1962a) demonstrated that a range of data sets appeared to conform to what he termed the canonical lognormal, which was regarded as an empirical hypothesis rather than a mechanistic explanation. Following May's (1975) detailed treatment of the canonical hypothesis, Sugihara (1980) proposed a model of sequential niche breakage that was designed to explain the underlying mechanisms. Recent studies on the abundance patterns of British birds (Nee et al. 1991, Gregory 1994) show that these data conform to Sugihara's model, strengthening the suggestion that this model is an adequate working hypothesis to explain relative abundance patterns of large assemblages in general.

On the other hand, as a related line of investigation in this discipline, attention has also been drawn to 'niche-apportionment' models (sensu Tokeshi 1990, 1993) where species abundances are considered to be associated with different processes of niche division. As the idea of common niche space is more easily applicable to taxonomically close species, these models have been applied mainly to assemblages with relatively small numbers of species (Tokeshi 1990, Schmid 1995). Whilst Sugihara's model is considered as a version of niche apportionment, other models of this genre have not been extended to assemblages with large number of species. Thus, for a decade and a half since Sugihara (1980) made an important attempt, no mechanistic model has emerged to offer an alternative explanation

for relative abundance patterns in species-rich assemblages. In addition, there exists a substantial amount of ambiguity and confusion about the nature of Sugihara's model and its relationships with some niche apportionment models of Tokeshi (1990). The objectives of the present paper are, firstly, to clarify in detail the basis of Sugihara's model in relation to other niche apportionment models, particularly the Random fraction model (Tokeshi 1990), and secondly, to present a new model termed the Power fraction model as an alternative, ecologically more plausible explanation of relative abundance patterns in species-rich assemblages.

Sugihara's model revisited

Sugihara (1980) envisaged successive niche division to occur with division ratios taking a triangular frequency (probability) distribution centred around 0.75:0.25 (Fig. 1a), based on some observations of two-species systems involving barnacles and fish. Setting aside the question of a tenuous link between the limited nature of the data on which this logic is based and a supposed triangular distribution of division ratios, Sugihara assumed further that expected (average) values of abundances under such a system of niche division could be obtained by applying a fixed division ratio of 0.75:0.25 (Fig. 1b). Thus, for heterogeneous assemblages with large numbers of species, the expected values of abundance and the standard deviations of log abundance were obtained by simulating the niche division sequence with the fixed ratio of 0.75:0.25 in his work.

The validity of the supposition that the fixed ratio (0.75:0.25) is a convenient approximation (Fig. 1b) to what one might expect as an average in a large universe under a more general triangular frequency distribution (Fig. 1a) can be tested by performing simulations in two different manners, adopting either the fixed ratio of 0.75:0.25 or a triangular distribution as shown in Fig. 1. The results of such simulations (up to 1000 replications for different values of species richness, S, for each case) clearly demonstrate that the fixed ratio assumption and the triangular assumption do not lead to a convergent pattern (Fig. 2), indicating that the above supposition is untenable. In theory, it is indeed apparent that once a division occurs to form two fragments of inequitable sizes (i.e. the ratio exceeding 0.75 for the larger of a pair), that inequitability is unlikely to be reversed completely at a later stage to restore the situation where the 0.75:0.25 ratio always prevailed, within a finite number of divisions. In other words, the cumulative effect of occasional inequitable divisions (i.e. formation of very small fragments) is to augment variability in niche size over and above what is expected from a breakage process governed by a fixed division ratio. Thus, the triangular probability assumption will lead to a higher

inequitability or a larger standard deviation (σ) of log abundance values than the fixed-ratio assumption (i.e. the curve for the former lies above that of the latter in Fig. 2). Although it may be tempting to argue theoretically that an increasing number of species following the same triangular rule will tend to converge to a distribution clustered around 0.75, there is little to substantiate that this proposition is valid and applicable to natural assemblages with a finite number of species. Therefore, Sugihara's (1980) demonstration that his sequential breakage model agreed with a miscellany of data on species-rich assemblages (cf. Fig. 7 of his paper) should be interpreted as being based upon the assumption of a static, fixed division ratio of 0.75:0.25 which he em-
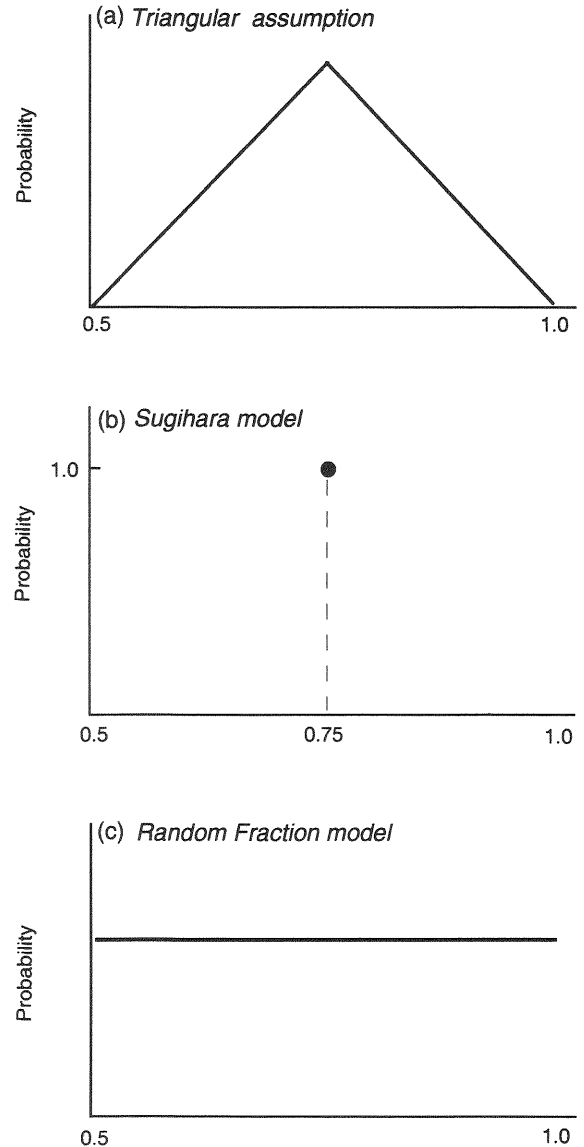

Fig. 1. Probability distribution of division points along niche axis (0.5 to 1.0) under three different hypotheses.
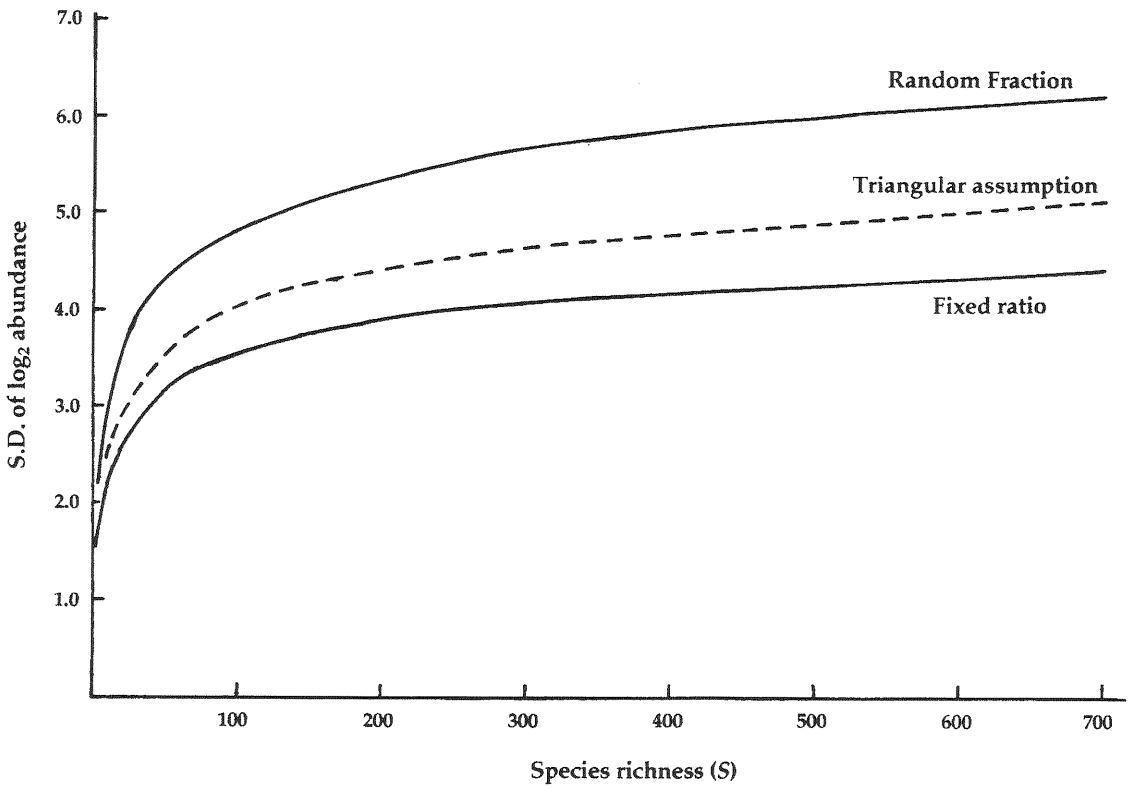
Fig. 2. Relationship between standard deviation (SD) of $\log_2$ abundance and species richness S in the Random fraction, the triangular assumption, and the fixed ratio (0.75:0.25) division models.
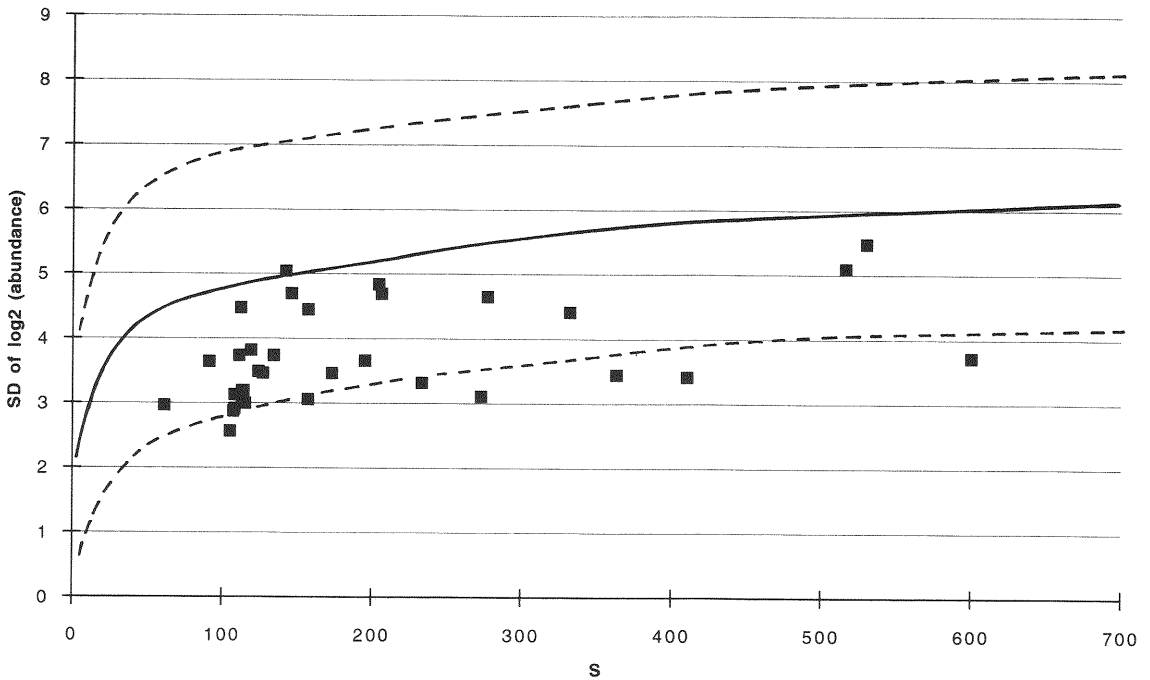

Fig. 3. Random fraction model fitted to abundance data on miscellaneous species-rich assemblages (data from Preston (1948, 1962a, b), Patrick (1968), Patrick et al. (1954), Edgar (1987), Nee et al. (1991), Gregory (1994)). Continuous and broken lines represent mean ± 2 S.D. of σ (standard deviation of $\log_2$ abundance) from the model. Theoretical values were obtained through numerical simulations (100–1000 replications) performed for different values of species richness, S.

ployed in his simulation, not as a representation of the triangular assumption. There is, on the other hand, a multitude of possibilities for the shape of a general triangular distribution, which may result in different patterns (cf. Sugihara 1982, Siegel and Sugihara 1983). Sugihara (1982) rightly considered such variability. Here, it should be recognised that niche division with a fixed ratio is qualitatively different from niche division with variable ratios, at least under the circumstances envisaged in Sugihara's 1980 paper.

This leads to another important question about the relationship between these models (the term Sugihara's model is hereafter restricted to the model with the fixed division ratio, his 'original' model being referred to simply as the 'triangular' model, to avoid confusion) and the Random fraction model (Tokeshi 1990). In the RF model, division ratio can take any value with equal probability, i.e. a uniformly random value assumed for the division ratio (Fig. 1c). A comparison between simulation results of the RF model with those of the Sugihara model and the triangular model shows that the triangular model produces values which lie between the RF model and the Sugihara model (Fig. 2). Indeed, it should be pointed out that Sugihara (1980) himself explicitly discussed and rejected the hypothesis embodied here as the RF model, arguing that it represented an artefact of classification (G. Sugihara pers. comm.). Thus, Nee et al.'s (1991) statement that Sugihara's model is the only one that can perform well with both small and large data sets (the small data referring to Tokeshi's (1990) work) is incorrect, as Tokeshi's (1990) data on a chironomid community conformed to the Random fraction model (in addition to the Random assortment model), but not to the Sugihara model. It is therefore important to stress that the Random fraction model is a model with an independent identity, which is distinct from the Sugihara model and constitutes a useful point of reference within the spectrum of niche apportionment models (Tokeshi 1993).

A major problem with Sugihara's approach can then be summarised as follows: fit to data and biological reality do not neatly go together. Good conformity to data, as was shown in his own simulation (Fig. 7 in Sugihara (1980)), depends upon the supposition that sequential divisions always occur with the static division ratio of 0.75:0.25, a condition that is highly unlikely to hold in ecological communities with large numbers of species through both evolutionary and ecological time. Instead, if one adheres to Sugihara's original idea of a triangular probability distribution of division ratios, the resultant pattern of relative abundances does not necessarily show a perfect fit to data (save with different patterns of triangular distribution, Sugihara (1982)). Furthermore, it tends to approach towards what is expected from the Random fraction model which Sugihara rejected in the first place. If this is the case, the argument can then be phrased from a slightly different perspective, with reference to the RF model. It is notable that a good proportion of the data points from various assemblages lies within the expected mean – 2SD band (but not in the mean + 2SD band) of the RF model (Fig. 3), suggesting that this model can indeed account for patterns in some cases. On the other hand, the triangular probability distribution which Sugihara (1980) advocated as biologically more realistic a proposition improves on the RF model only moderately. Under the circumstances, the RF model remains as a valid, parsimonious explanation (i.e. no constraint upon division ratios) of abundance patterns in natural communities, as well as being a theoretically useful reference within the family of niche apportionment models. This leads to a possibility of a new hypothesis.

The Power fraction model

The above considerations have highlighted some theoretical and conceptual complications of Sugihara's (1980) proposition. Further, the somewhat ambiguous nature of the relationship between various possibilities of the triangular assumption and the fixed ratio assumption cannot easily be resolved with reference to a limited range of empirical data. This is not to negate the historical importance of Sugihara's perceptive work, but there is clearly some scope for tackling the issue from different per

The new model follows the concept of niche apportionment, where total niche space (or multi-dimensional resource volume) is sequentially divided (Tokeshi 1990, 1993). Notwithstanding the precise nature of such a total niche, members of any ecological assemblage, small or large, share at least a volume of space which is ultimately limited on earth. The new model is best illustrated together with two earlier niche apportionment models, the Random fraction (RF) model and the MacArthur fraction (MF) model (Fig. 4). In these models, one of the existing niche fragments (or species represented by them) is selected with different probability weighting and divided at random into two fragments. In the new Power fraction (PF) model, the probability of selection for a subsequent division is proportional to the sizes of existing niche fragments raised to the exponential (power) parameter k, where k is in the range of 0 to 1. After selection of a niche fragment with such probabilistic weighting, the chosen fragment is divided at random into two smaller fragments, and the process is repeated. In contrast to Sugihara's model where the division ratio is fixed at 0.75:0.25, the PF model envisages division to occur with any ratio, i.e. uniform randomness of breakage points. A power fraction model with $k = 0$ corresponds to the RF model and one with $k = 1$ to the MF model.

Fit of the PF model to data from species-rich assemblages is good. As an example, Fig. 5 shows that the
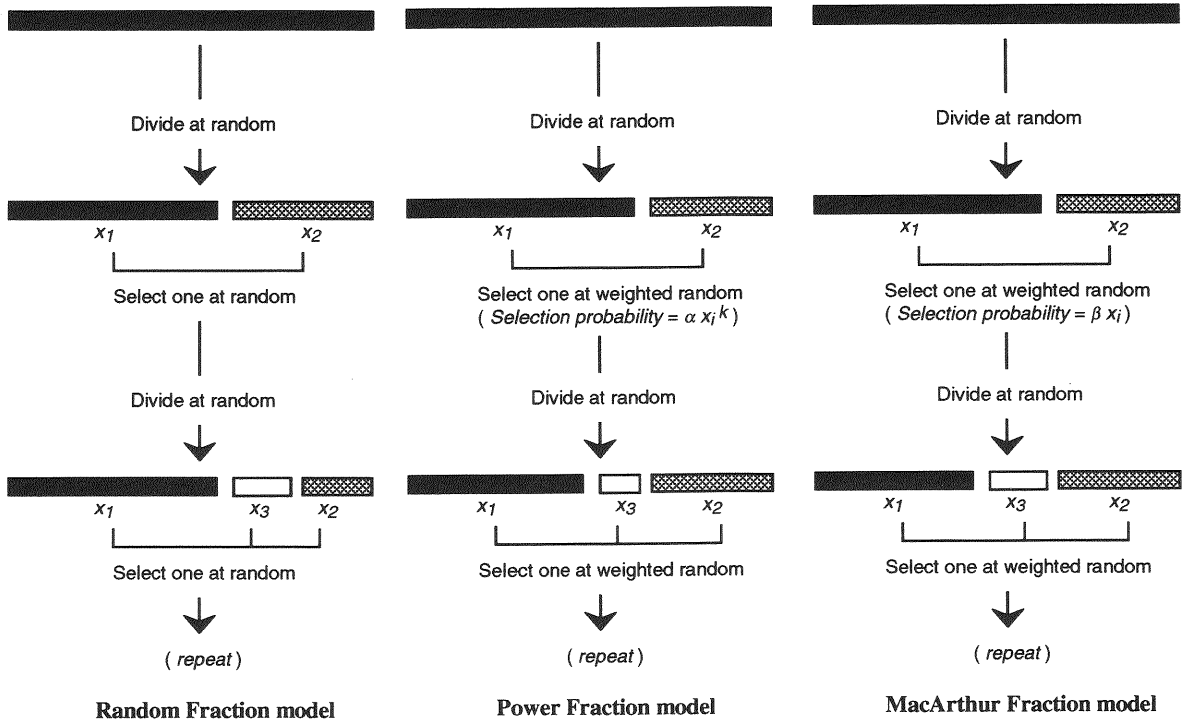
Fig. 4. Schematic representation of the Power fraction model (middle), together with the Random fraction and MacArthur fraction models. In the Random fraction model, species with different niche sizes/abundances have the same chance of being selected for a subsequent niche division (speciation or invasion by a new species), i.e. probability weighting is zero. In the Power fraction model, the probability of selection is proportional to niche size (or abundance) raised to a power exponent k ($0 \leq k \leq 1$). Note that α, a constant, is common to all the species in an assemblage and $\Sigma \alpha x_i^k = 1$ where x_i denotes niche size/abundance of species i. In the MacArthur fraction model, the probability of selection is proportional to x_i ($\Sigma \beta x_i = 1$ where β is a constant). Power fraction with $k = 0$ is equivalent to RF, and PF with $k = 1$ is equivalent to MF.
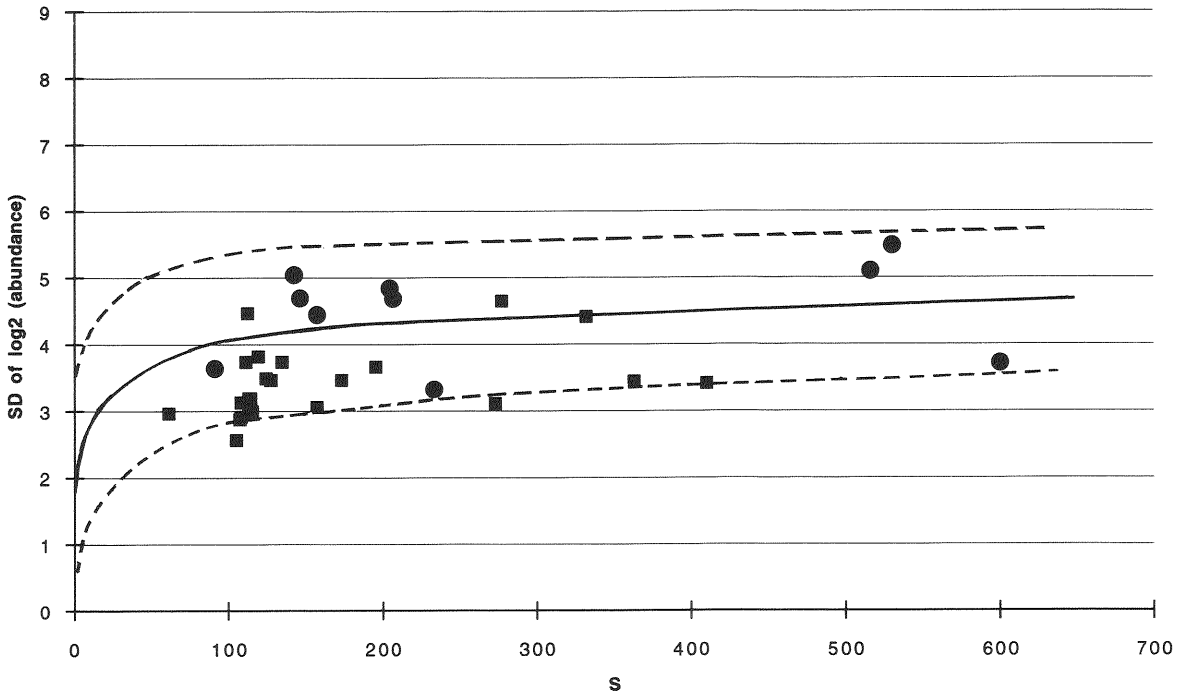

Fig. 5. Power fraction model with $k = 0.05$ fitted to abundance data on miscellaneous species-rich assemblages (bird assemblages are shown by ● ; data as in Fig. 3). Continuous and broken lines represent mean ± 2 S.D. of s (standard deviation of $\log_2$ abundance) from the model. Theoretical values were obtained through numerical simulations (100–1000 replications) performed for different values of species richness, S.
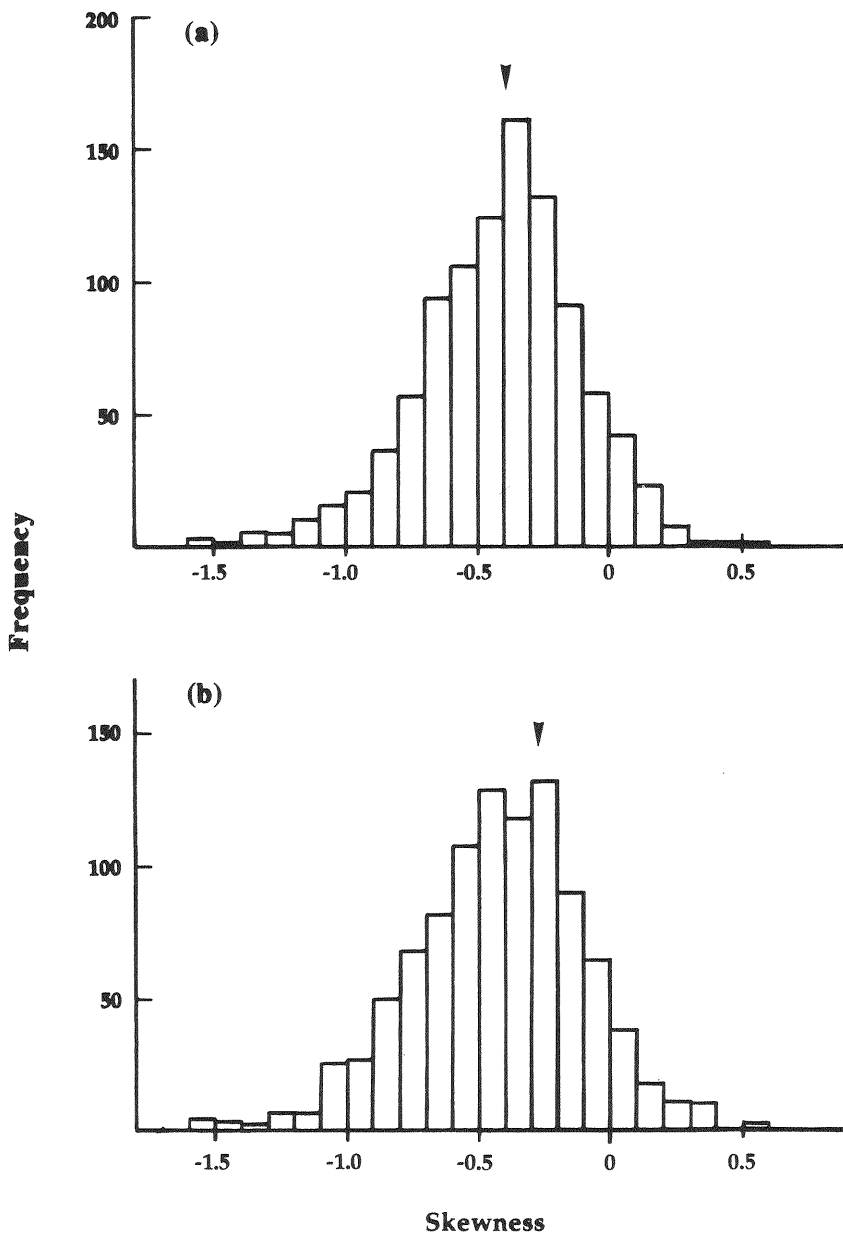
model with $k = 0.05$ encompasses the majority of data points within mean ± 2 S.D. bands with reference to standard deviations (σ) of 'octaves' or $\log_2$ abundances plotted against total number of species, S (note that Sugihara (1980) first adopted this approach for examining fit of his model to data). Perhaps more importantly than a general fit, high-quality data where abundances of rare species in an assemblage are accurately estimated, e.g. bird data in general and those of British breeding birds from the BTO (British Trust for Ornithology) surveys in particular, lie well within model expectations (analyses of the BTO data: $\sigma = 4.7$, $S =$

146 (Nee et al. (1991), based on Marchant et al. (1990)) and $\sigma = 4.45$, $S = 157$ (Gregory (1994), based on Gibbons et al. (1993) which is considered a more accurate data set than Marchant et al. (1990)). Furthermore, skewness (μ^3/σ^3, where μ^3 is the third central moment) of these data (-0.396 and -0.281, respectively) also agrees with expectations from the PF model with $k = 0.05$ (mean of 1000 simulations for $S = 146$ and 157, $\mu^3/\sigma^3 = -0.419$ and -0.431, respectively; left-skewness clearly observed in Fig. 6). It is also notable that these bird data tend to have higher values of σ than values for other assemblages (Fig. 5). An improve-
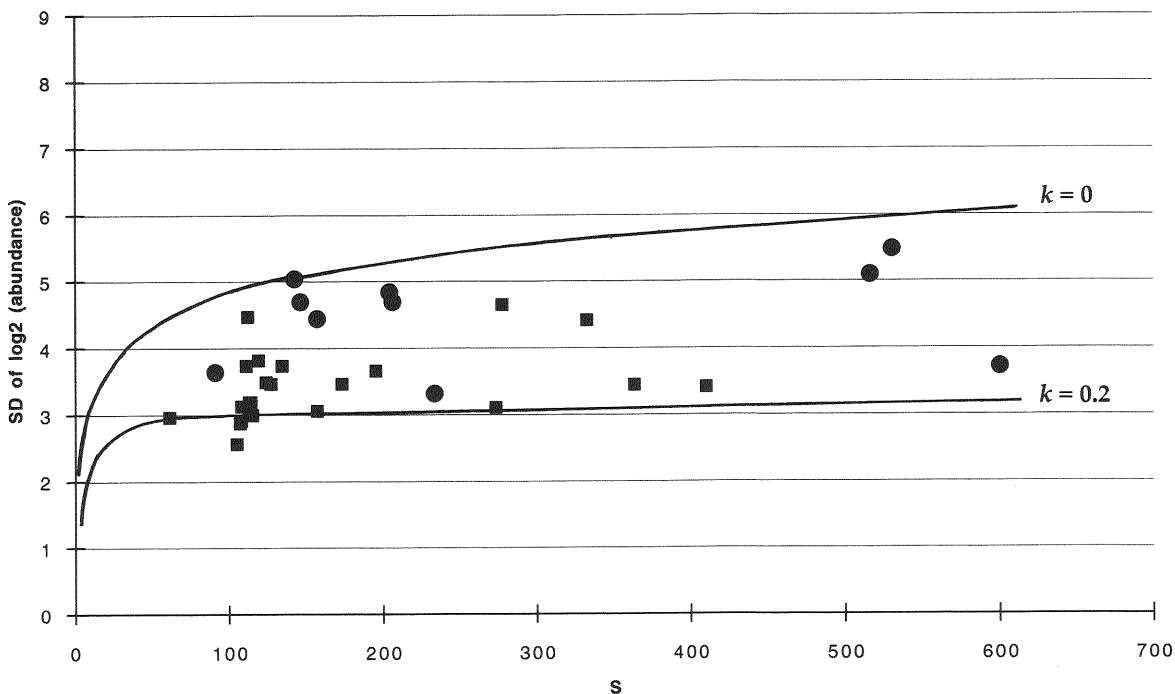
Fig. 7. Power fraction model with $k = 0$ (upper line) and $k = 0.2$ (lower line) fitted to abundance data on species-rich assemblages (the same as in Fig. 3).

ment in data quality of species-rich assemblages implies that the abundances of rare species are more accurately represented (e.g. inclusion of many species with few individuals, that have previously been overlooked or amalgamated with other species), which would generally lead to an increase in σ. Thus, there are high possibilities that relatively low values of σ in the data set represent under-estimations.

Instead of applying a single PF model with a fixed parameter to the entire data set, it is also possible to fit the model with different parameter values to different data. If mean values of σ are considered, data points appear to lie between $k = 0$ and $k = 0.20$ (Fig. 7), indicating that the PF model with $k \sim 0-0.2$ could mostly account for the observed abundance patterns of large assemblages.

The fact that the PF model with $k \sim 0.05$ or $k \sim 0-0.2$ fitted the data suggests that assemblages may be formed by a sequential niche apportionment process where the probability of successive niche division (or invasion of existing niche space) tends to be higher (but only slightly so) for species with larger niches/higher abundances. That species with higher abundances and larger geographical ranges are more likely to generate new species was explicitly stated by Darwin (1859) and is in agreement with some fossil evidence (Jablonski 1987). Furthermore, environmental barriers that could eventually affect how a species would split into two may appear anywhere in the species' distributional range, thereby rendering the division ratio widely variable, as has been

assumed in the PF model. Thus, the model is not inconsistent with ecological and evolutionary perspectives.

In addition to ecological/evolutionary plausibility as mentioned above, an advantage of the new model concerns the fact that it may be formulated as either a global model or a community-specific model. This dichotomy has an important implication for community analyses (Tokeshi 1993), the former approach implicitly assuming that different communities follow the same governing rule and the latter accepting a divergence of patterns and mechanisms. The application of a single model with fixed parameter values to a collection of data covering a wide range of taxa and assemblages corresponds to the former, as exemplified by attempts to fit Sugihara's fixed ratio model or the PF model with $k = 0.05$. In contrast, if plurality in community pattern is a norm (Schoener 1986), it is more appropriate to fit a model with different parameter combinations to different data sets. The PF model allows this with variable k (Fig. 7). Such an approach may eventually indicate a convergence of parameter values, which will constitute more powerful evidence of the existence of a global pattern, if it does exist.

The PF model with the parameter k in the range of $0-0.2$ seems to suggest one principle that, on average, the probability of speciation or invasion is proportional to a fractional power (<0.2) of a species' current abundance. This is naturally based on an assumption that patterns of abundances in contemporary communities reflect the relative abundances of species over evolu-

tionary time, although the exact identity of species in a given assemblage may have changed. Whether this is true or not is an interesting question to be considered in future studies of palaeobiology and evolutionary ecology.

At the very least, models that allow community-specific analyses are conceptually and practically more flexible and useful in suggesting hypotheses. Furthermore, the Power fraction model has a wider theoretical implication in the sense that this model may be considered to encompass other niche apportionment models, if its parameter k is taken from minus infinity to plus infinity. Such an integrative approach to species abundance patterns has not emerged before in this discipline. These aspects make it more interesting to apply of the Power fraction model to other high-quality data of both small and large assemblages, as they become available; such comparative studies may provide an insight into how biodiversity has been generated in different systems.

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