REVIEW AND SYNTHESIS

Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework

Brian J. McGill,[1]* Rampal S. Etienne,[2] John S. Gray,[3] David Alonso,[4] Marti J. Anderson,[5] Habtamu Kassa Benecha,[2] Maria Dornelas,[6] Brian J. Enquist,[7] Jessica L. Green,[8] Fangliang He,[9] Allen H. Hurlbert,[10] Anne E. Magurran,[6] Pablo A. Marquet,[10,11,12] Brian A. Maurer,[13] Annette Ostling,[4] Candan U. Soykan,[14] Karl I. Ugland[3] and Ethan P. White[7]

Abstract

Species abundance distributions (SADs) follow one of ecology's oldest and most universal laws – every community shows a hollow curve or hyperbolic shape on a histogram with many rare species and just a few common species. Here, we review theoretical, empirical and statistical developments in the study of SADs. Several key points emerge. (i) Literally dozens of models have been proposed to explain the hollow curve. Unfortunately, very few models are ever rejected, primarily because few theories make any predictions beyond the hollow-curve SAD itself. (ii) Interesting work has been performed both empirically and theoretically, which goes beyond the hollow-curve prediction to provide a rich variety of information about how SADs behave. These include the study of SADs along environmental gradients and theories that integrate SADs with other biodiversity patterns. Central to this body of work is an effort to move beyond treating the SAD in isolation and to integrate the SAD into its ecological context to enable making many predictions. (iii) Moving forward will entail understanding how sampling and scale affect SADs and developing statistical tools for describing and comparing SADs. We are optimistic that SADs can provide significant insights into basic and applied ecological science.

Keywords

Environmental indicators, macroecology, scientific inference, species abundance distributions.

[1]*Department of Biology, McGill University, 1205 Ave Dr Penfield, Montreal, QC H3A 1B1, Canada*

[2]*Community and Conservation Ecology Group, University of Groningen, Haren, The Netherlands*

[3]*Department of Biology, University of Oslo, Oslo, Norway*

[4]*Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, MI, USA*

[5]*Department of Statistics, University of Auckland, Auckland, New Zealand*

[6]*Gatty Marine Laboratory, University of St Andrews, Fife, Scotland*

[7]*Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, AZ, USA*

[8]*School of Natural Sciences, University of California Merced, Merced, CA, USA*

[9]*Department of Renewable Natural Resources, University of Alberta, Edmonton, Alberta, Canada*

[10]*National Center for Ecological Analysis and Synthesis, University of California Santa Barbara, Santa Barbara, CA, USA*

[11]*Center for Advanced Studies in Ecology & Biodiversity (CASEB), Departamento de Ecología, Facultad de Ciencias Biolígicas, Pontificia Universidad Católica de Chile, Alameda 340, Santiago, Chile*

[12]*Instituto de Ecología y Biodiversidad (IEB), Departamento de Ciencias Ecológicas. Facultad de Ciencias, Universidad de Chile. Casilla 653, Santiago, Chile*

[13]*Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI, USA*

[14]*School of Life Sciences, Arizona State University, Tempe, AZ, USA*

*Correspondence: E-mail: mail@brianmcgill.org

INTRODUCTION

What is an SAD?

A species abundance distribution (SAD) is a description of the abundance (number of individuals observed) for each different species encountered within a community. As such, it is one of the most basic descriptions of an ecological community. When plotted as a histogram of number (or percent) of species on the *y*-axis vs. abundance on an arithmetic *x*-axis, the classic hyperbolic, 'lazy J-curve' or 'hollow curve' is produced, indicating a few very abundant species and many rare species (Fig. 1a). In this form, the law appears to be universal; we know of no multispecies community, ranging from the marine benthos to the Amazonian rainforest, that violates it. When plotted in other fashions, such as log-transforming the abundances (Fig. 1b), more variability in shape occurs, giving rise to considerable debate about the exact nature of SADs. Nevertheless, the hollow-curve SAD on an arithmetic scale is one of ecology's true universal laws.

To be precise, we define an SAD as a vector of the abundances of all species present in a community. Often, the SAD is presented visually in a rank-abundance diagram (RAD; Fig. 1c) where log-abundance is plotted on the *y*-axis vs. rank on the *x*-axis. This plot contains exactly as much information as the vector of abundances. In contrast, histograms (Fig. 1a,b) involve binning and thus a loss of information. In our definition, the term 'community' is vague (Fauth *et al.* 1996), and we do not choose to give a precise definition here, but the choice becomes important when we study the role of scale and sample size in SADs (discussed later). The two most salient features of the SAD are the fact that the species are not 'labelled' by having a species identity attached to the abundance and that zero abundances are omitted. This loss of labels allows for comparison of communities that have no species in common, for example, a freshwater diatom community and a tropical tree community. At the same time, SADs enable nuanced questions and comparisons such as asking which community has a higher proportion of rare species
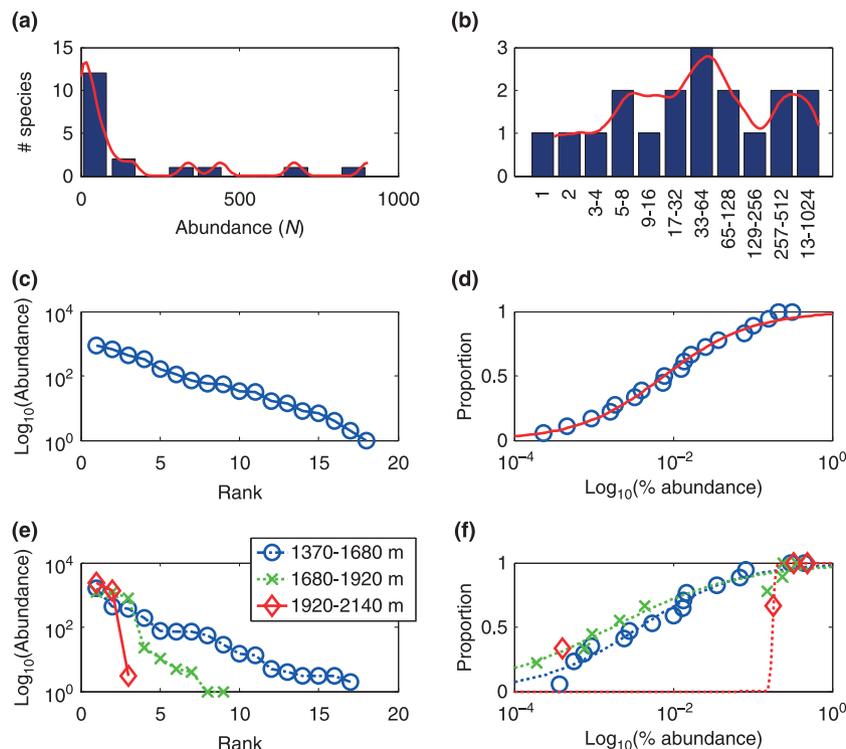

Figure 1 Different ways to plot SADs. Abundance data for trees collected by Whittaker in the Siskiyou Mountains (Whittaker 1960) is replotted here in three different formats. (a) A simple histogram of number of species vs. abundance on an arithmetic scale. A smoothed line is added to highlight the overall shape. (b) A histogram with abundance on a log-scale. Note the traditional format is to use $\log_2$. (c) A rank-abundance diagram (sometimes called a RAD). Log abundance (here $\log_{10}$ to make the reading of values easier) is plotted against the rank (1 = highest abundance out to S = number of species for the lowest abundance). (d) An empirical cumulative distribution function (ECDF) with a NLS logistic line fit through the data. Note that both the *x*- and *y*- axes are scaled into percentages. (e) A rank-abundance plot for data from three different elevational bands showing different shapes observed. (f) The same three elevational bands now plotted as an ECDF. Same colour/symbol legend as Fig. 1e.

Table 1 This table describes three common descriptions of community structure in increasing degrees of accuracy in parallel with decreasing degrees of simplicity. Species abundance distributions are intermediate on these scales

Complexity	Data	Example	Strengths	Weaknesses
Low	Univariate measures such as species richness, S; Shannon evenness, J; Simpson diversity, 1-D; Number of individuals, N	$S = 5$, $N = 17$, $J = 1.20$, $1\text{-}D = 0.60$, # singletons = 2	1. Can compare between communities that have few or no species in common 2. Easy to understand	1. High loss of information 2. Depends on sample size which is not included in the measure
Intermediate	Species abundance distribution (SAD) – a vector of numbers with zero abundances eliminated and no species labels attached, possibly displayed as a curve in a 2-D plot	{10 3 2 1 1} (plot of values 10, 3, 2, 1, 1 on a log-scale axis from 1 to 10)	1. Can compare between communities that have few or no species in common (can even compare, e.g., freshwater diatoms to tropical birds) 2. Easy to understand 3. Moderate retention of information – can still look at questions such as relative proportion of rare, intermediate, and common species 4. Visual comparison of two communities possible 5. Information about sample size is incorporated in the SAD	1. Some loss of information 2. Comparing two communities not as easy as comparing with univariate measures
High	Species labeled and zero abundances retained, e.g. Q-mode matrix with species in rows, sites in columns, and abundance in cells. Used in analyses such as ordination	*Table:* Site 1 / Site 2 *S. primus* 10 / 8 *S. secundus* 3 / 4 *X. maximus* 2 / 1 *X. minimus* 1 / 2 *Q. singularis* 1 / 0	1. Full retention of information 2. Ability to track changes in abundance of individual species	1. Cannot compare communities that are not largely similar 2. Difficult to understand (presented as table of numbers or as output of multivariate statistics such as ordination)

rather than just asking which community is more species rich. In general, the SAD can be conceived of as falling in an intermediate position on a spectrum of increasingly complex descriptions of a community (Table 1).

Why are SADs important?

Not only is the hollow-curve SAD universal, but it is a surprising, counterintuitive and therefore informative law. Surely a *prima facie* null expectation is for abundances to be more or less evenly distributed with some minor variation because of body size, life history etc (i.e. normal with a mean approximately equal to the number of individuals divided by the number of species). In fact SADs are so uneven that this null expectation is not even useful in studying SADs. Why? If we can explain this high degree of unevenness, then we likely will be in a position to make strong statements about which mechanisms structure communities, be they species interactions, random chance or some other factor. Thus understanding SADs is a major stepping stone to understanding communities in general.

The raw data underlying an SAD (i.e. a census of the number of individuals per species or even per morphospecies) is among the most commonly collected data in ecology (although SAD data is lacking for many types of communities such as bacteria or mycorrhizae, and for larger organisms

complete censuses are empirically daunting to gather at even intermediate spatial scales such as 50 ha). The overall availability of data combined with the intermediate complexity of SADs (Table 1), their potential for comparison among disparate communities, and their visual nature have made SADs very popular in ecological research. SADs are commonly taught in undergraduate ecology and management classes. The SAD is also pivotal in conservation – described as the 'science of scarcity' (Soule 1986); the relative terms 'common' and 'rare' are given a clear definition in the context of an SAD. In short, the SAD has played and is likely to continue to play a central role in ecology.

Brief history

It is unclear exactly when ecologists first began to measure SADs quantitatively. Yet the existence of a few very common species and many very rare species was an obvious fact even to casual observation. Audubon in the 1800s was aware that birds in North America have abundances that vary by as much as seven orders of magnitude (McGill 2006). Darwin (1859) noted 'Who can explain why one species ranges widely and is very numerous, and why another allied species has a narrow range and is rare? Yet these relations are of the highest importance, for they determine the present welfare and, as I believe, the future success and modification

of every inhabitant of this world'. The first formally published quantitative analysis of an SAD of which we are aware is by Raunkiaer (1909) (although technically he measured occupancy rather than abundance). By the 1940s the use of histograms had become well-established (Fisher *et al.* 1943; Preston 1948) and the use of a log-transformed abundance (Preston 1948) was introduced. The RAD plot was first introduced by MacArthur (1957). Note that the empirical cumulative distribution (ECDF) is not often used, but is mathematically equivalent to the RAD involving only a swapping and rescaling of the axes. Fig. 1a–c shows the three different ways these data are commonly plotted and Fig. 1d shows the ECDF. Two reviews on SADs were written in the 1960s and 1970s that implied we had worked out the basic patterns and processes of SADs (Whittaker 1965; May 1975). But later reviews (Gray 1987; Marquet *et al.* 2003) express a belief that there has been a disappointing lack of progress in the study of SADs.

We now provide more detail in the next three sections covering, in order, theoretical, empirical and statistical developments in the analysis of SADs. A healthy scientific field will advance roughly in parallel in each of these three areas. We conclude with a section identifying ways in which SADs have failed to achieve parallel advancement in these areas and suggest important directions to move forward.

THEORETICAL DEVELOPMENTS IN SADS

Classical theoretical developments

The first theory attempting to explain the mechanism underlying hollow-curve SADs was by Motomura (1932). He pointed out that a sequential partition of a single niche dimension by a constant fraction leads to the geometric distribution. Fisher *et al.* (1943) argued for the logseries distribution as the limit of a Poisson sampling process from a gamma distribution (where the gamma was chosen only because of its general nature). Kendall (1948a) put the logseries on a more mechanistic footing by deriving it from birth-death-immigration models. Preston (1948) argued for a modified lognormal on the basis of the central limit theorem. MacArthur (1957) built on Motomura's idea of partitioning a one-dimensional niche but used a random stick-breaking process. This would seem to have set the stage for a clear test with empirical data. Each theory made distinct predictions: the geometric model predicts extremely uneven abundances, broken stick predicts extremely even abundances, while lognormal and logseries are intermediate with distinct predictions about the proportions of very rare species – high in logseries, low in lognormal. But an empirical resolution has not occurred. With the possible exception of the broken stick, none of the four classical hypotheses have been eliminated. Instead, we have seen

literally dozens of new hypotheses added without elimination of older hypotheses.

Proliferation of models

Starting in the 1970s and running unabated to the present day, mechanistic models (models attempting to explain the causes of the hollow curve SAD) and alternative interpretations and extensions of prior theories have proliferated to an extraordinary degree (May 1975; Gray 1987; Tokeshi 1993; Marquet *et al.* 2003). Broadly speaking, we identify five families of SAD models with over 40 members (see Table 2 for an incomplete list; see also Marquet *et al.* 2003 for a similar analysis):

(1) *Purely statistical*: purely statistical theories take some combination of the continuous gamma and lognormal distributions with the discrete binomial, negative binomial, and Poisson distributions. The lognormal has many versions (see Table 2); we recommend using either the simple, untruncated continuous lognormal because of the extreme ease with which it is fit (mean and standard deviation of log-transformed data) or the Poisson lognormal because of its technical merits (Bulmer 1974; Etienne & Olff 2005).

(2) *Branching processes*: when dealing with biological processes, individuals are always derived from ancestor individuals. This suggests a random-branching process as a model.

(3) *Population dynamics*: a variety of population dynamic models arrayed along a spectrum from purely deterministic to purely stochastic can also produce realistic SADs.

(4) *Niche partitioning*: another group of models is based on dividing up a one-dimensional niche space. The oldest SAD model is of this type (Motomura 1932).

(5) *Spatial distribution*: one can build spatial models of SADs if one conceives of the SAD as counting all the individuals falling within a particular region of space and if one knows (or can model statistically): (i) the spatial distribution of individuals within a species and (ii) the distribution of species relative to each other.

Several of these families overlap. For example, neutral models (Caswell 1976; Bell 2000; Hubbell 2001) are stochastic population dynamic models but also branching process models (Etienne & Olff 2004b), and the lognormal can be the limit of population dynamics (Engen & Lande 1996b) or niche partitioning (Bulmer 1974; Sugihara 1980).

Major theoretical controversies

Given the proliferation of theories there has been considerable debate (e.g. Alonso *et al.* 2006; Nekola &

Table 2 Dozens of theories attempting to explain (and in most cases provide a mechanism to) the hollow curve SAD exist. This table briefly summarizes them and organizes them into related families. For a similar analysis performed a few years earlier see Marquet *et al.* (2003)

Family	SAD	Comments
Purely statistical	1. Logseries	Fisher *et al.* (1943) used a gamma distribution to describe the underlying 'true' abundance for purely empirical reasons, and then using the gamma random variable as the parameter of a Poisson distribution to describe the discrete samples that occur in finite real world samples gives a negative binomial distribution (which he then truncates the 0-abundance category and takes a limit). Boswell & Patil (1971) later showed that many other arguments can also produce the logseries.
	2. Negative binomial	Brian (1953) is one of the few people to use the seemingly obvious negative binomial (usually 0-truncated)
	3. Gamma	A variety of population dynamic models lead to a gamma distribution (Dennis & Patil 1984; Engen & Lande 1996a; Diserud & Engen 2000), which seems to fit some data well (Plotkin & Muller-Landau 2002)
	4. Gamma-binomial or Gambin	Compounding the gamma with a binomial sampling process (cf. the Poisson compounded with the gamma to produce the logseries) gives a one parameter distribution where the single parameter seems to be a good measure of the environmental complexity (Ugland *et al.* 2007)
Purely statistical (lognormal subfamily)	5. Lognormal I – Preston's discrete, binned approximation	A discretized version of the lognormal (Preston 1948; Hubbell 2001) is probably no longer justified given modern computing power
	6. Lognormal II – true continuos lognormal	The original lognormal (Galton 1879; McAlister 1879; Evans *et al.* 1993) which has received extensive application to ecology (Gray 1979; Dennis & Patil 1984, 1988; McGill 2003c)
	7. Lognormal III – left truncated (veiled) lognormal	As in number 6, but with left truncation (Cohen 1949) to match Preston's idea of unveiling. Has rarely been used in practice (and which in fact usually does not fit the data as well as the untruncated version McGill 2003a)
	8. Lognormal IV – Poisson lognormal	Mixes the lognormal with the Poisson (cf. the logseries which mixes the gamma and the Poisson; Bulmer 1974; Kempton & Taylor 1974). Requires an iterative likelihood method on a computer to fit which is often not available in standard statistical packages (Yin *et al.* 2005), and is sometimes confusingly called a truncated lognormal (Kempton & Taylor 1974; Connolly *et al.* 2005).
	9. Lognormal V – Delta lognormal	A mixture of the continuous lognormal and a Bernoulli variable to allow zeros to occur with a probability P (Dennis & Patil 1984, 1988)
Branching process	10. Generalized Yule	Yule (1924) applied what is now known as the Galton-Watson branching process to model the number of species within a genus (which has a distribution similar to individuals within species). Kendall (1948b) and Simon (1955) generalized this work and used it as a model of population dynamics and abundance. Chu & Adami (1999) analysed this again in an ecological context, and Nee (2003) showed that this distribution provides extremely good fits to SADs.
	11. Zipf-Mandelbrot	Using a different type of branching process known as a scaling (or fractal) tree, Mandelbrot (1965) generalized Zipf's (1949) Law in linguistics to produce the Zipf-Mandelbrot distribution. This has been applied to SADs by several authors (Frontier 1985; Wilson 1991; Frontier 1994, 1985; Wilson *et al.* 1996).
	12. Fractal branching model	Mouillot *et al.* (2000) introduce a fractal branching (tree-like) extension to the niche pre-emption model (#19)
Population dynamics	13. Lotka-Volterra	The generalized Lotka-Voltera models with random parameters can produce a hollow curve (Lewontin *et al.* 1978; Wilson *et al.* 2003).
	14. Hughes	A detailed single species population dynamic model with random parameters (Hughes 1986) can produce hollow curves

Table 2 (*continued*)

Family	SAD	Comments
	15. Stochastic single species	Population dynamic models with stochastic noise can produce hollow curve SADs (Tuljapurkar 1990; Engen & Lande 1996a; Diserud & Engen 2000; Engen *et al.* 2002). Most of these models produce either a lognormal or a gamma distribution under quite general conditions on the population dynamics (Dennis & Patil 1984, 1988)
	16. Logistic-J	Dewdney (2000) has developed a simulation of random encounters and random transfer of resources that produces what he calls the logistic-J SAD.
Population dynamics (Neutral model subfamily)	17. Neutral	The ability of neutral models (with populations performing a coupled version of a random walk or drift) to produce SADs has excited much attention (Chave 2004; Alonso *et al.* 2006; McGill *et al.* 2006b). Bell (2000, 2001, 2003) and Hubbell (1979, 2001) have pushed this idea extensively recently, but it was shown much earlier by Caswell (1976) and Watterson (Watterson 1974) that with or without zero-sum dynamics neutral drift produces realistic SADs (Etienne *et al.* 2007a).
	18. Coalescent neutral theory	A coalescent version of neutral theory (Etienne & Olff 2004b; Etienne 2005) has shown that neutral population dynamics have some similarities to the branching processes described above.
Niche partitioning	19. Geometric or niche preemption	Motomura (1932) used a model where each species takes a constant fraction of the remaining resources.
	20. Broken stick	MacArthur (1957, 1960) developed the opposite model where the niche space is broken up simultaneously and with random fractions and is known as the broken stick model. This model has the distinction of being one of the very few SAD models ever developed to have been strongly rejected by its inventor (MacArthur 1966; 'Let us hope these comments do not draw additional attention to what is now an obsolete approach to community ecology, which should be allowed to die a natural death.'). Cohen (1968) showed that the same math of the broken stick could be produced by an exactly opposite set of biological assumptions from those of MacArthur.
	21. Sugihara	Sugihara (1980) crossed Motomura's (1932) and MacArthur's (1957) models by breaking the stick randomly but in sequential fashion. Nee *et al.* (1991) showed this produced realistic left skew.
	22. Random fraction	Tokeshi (1993, 1996) has since developed a variety of niche apportionment models with various combinations of models 19–21.
	23. Spatial stick breaking	Marquet *et al.* (2003) explored the consequences of adding spatial structure to niche breakage models.
Spatial distribution of individuals	24. Continuum	Several authors (Gauch & Whittaker 1972; Hengeveld *et al.* 1979) showed that the roughly Gaussian bell-curved shape of abundance across a gradient or species range produces hollow curve SADs in local communities since at any one point most species are found in the tail of their bell-curve across species while a few species are found in the peak of their bell-curve (thereby flipping the emphasis from local interactions between species to regional spatial processes of individual species). McGill & Collins (2003) expanded this theory and provided empirical evidence that this mechanism is in fact explaining as much as 87% of the variation in local abundances.
	25. Fractal distribution	Harte *et al.* (1999) showed that starting only with an assumption that the distributions of individuals within a species were self-similar across spatial scale could lead to a realistic SAD. Although the initial formulation was found to not have a good fit to the data (Green *et al.* 2003)
	26. Multifractal	Borda-de-Agua *et al.* (2002) extend the fractal distribution model to cover multifractals (fractal dimension changes with scale)
	27. HEAP	A newer model, also based on a different description of the distribution of individuals across space has been developed (Harte *et al.* 2005).

Brown 2007) over whether some of the several dozen models listed in Table 2 are 'better' types of models *a priori* than other models (independent of how well they fit the data). This is of course a normative statement, which depends heavily on one's criteria for judging models. And there are many possible criteria. Some of the non-empirical criteria for favouring one theory over another that have been invoked in the context of SADs include:

(1) Many favour more *mechanistic* theories (usually the statistical models are considered non-mechanistic), but there is debate about what constitutes a mechanism. Some consider neutral models that are derived from basic principles of population dynamics more mechanistic while others consider the niche partitioning models that are a bit more abstract and static, yet based on more 'realistic' biological assumptions to be more mechanistic.

(2) In a purely predictive paradigm (Peters 1991), *predictive success* takes priority over mechanism.

(3) Others prefer *parsimony* (Ockham 1495) and related issues of elegance and having few parameters.

(4) Some models develop or use extensive *mathematical machinery* that allow for many different predictions to be derived (such as the neutral models and the spatial distribution models).

(5) Some models have *parameters that can be easily estimated* independent of the SAD data one is trying to fit. In principle neutral theory can do this, but in practice this has not been performed successfully for neutral theory (Enquist *et al.* 2002; Ricklefs 2003; McGill *et al.* 2006b) or any other SAD model to our knowledge.

(6) The models also invoke varying *degrees of symmetry* among the species. Many consider requirements of symmetry undesirable because of obvious differences among species. The most extreme such assumption is the 'neutrality' assumption of neutral theory (Hubbell 2001). This symmetry has also been controversial in the derivation of the lognormal using the central limit theorem (CLT; May 1975; Pielou 1977; Ugland & Gray 1982; McGill 2003a; Williamson & Gaston 2005). But, in fact, all SAD models constructed so far necessarily make some assumption of symmetry or exchangeability between species. For example, the niche partitioning models treat all species as identical except for a single factor leading to pre-emption (often suggested to be order of arrival which is stochastic and independent of any species property). The resolution of this may lie in recognizing that there are ecological asymmetries but that species started from symmetric initial conditions and later evolved asymmetries (distinct life histories, physiology, and

population dynamics) in evolutionary time (Hubbell 2006; Marks & Lechowicz 2006).

Ultimately, which model approach is 'best' will depend on the question at hand. Predicting the rate of shifts in rarity over time would likely require a mechanistic model, perhaps based on population dynamics, while just predicting the proportion of rare species might be better served by a simple, easy to estimate statistical model.

Causes of the proliferation

As just described, there is room for more than one type of SAD model. However, we believe the main cause of the extensive proliferation has more to do with a failure to successfully test and reject theories with data. Successful branches of science use strong inference (Platt 1964) – within a general model category, theories face off against each other and the data pick a winner. The loser disappears to science's dustbin while the winning theory may then be refined through additional iterations. The ever increasing supply of new SAD theories without the rejection of any old theories is the diametric opposite of what Platt (1964) suggested and must be counted as a collective scientific failure. The central problem has been that while most theories make one and only one prediction – that SADs will be a hollow-curve, predicting a hollow curve alone cannot possibly be the basis of a decisive test between competing theories because all the theories make this prediction. In precise mathematical terms, SADs are 'necessary' but not 'sufficient' for testing mechanistic theories. Any theory that produces an SAD which is not a realistic hollow curve SAD must surely be rejected (e.g. Etienne *et al.* 2007b), but having a theory that produces a realistic hollow curve (even one that closely fits some empirical data set) is not sufficient to strongly support the theory. Further discussion on why SADs have failed to lead to strong inference can be found in Textbox 1 and in McGill (2003a) and Magurran (2005).

Historically, ecologists hoped that predicting subtle variations in the hollow curve would produce a decisive test. But this has not worked well. Robert H. Whittaker (1975) noted that 'the study of (SADs) has not produced the single mathematical choice … that the early work suggested might be possible' which was echoed by Gray (1987). This is in part because most attempts to evaluate SAD models have not been sufficiently rigorous. We believe that at a minimum, attempts to establish the superiority of a theoretically predicted SAD must pay careful attention to points 1, 3, 4, and 5 in Textbox 1. Specifically rigorous tests must compare multiple models (point 1) using multiple measures of goodness of fit (point 4) on multiple data sets (point 5). If one SAD theory emerges as clearly superior (point 3), then – perhaps – there is some justification for feeling a conclusion has been reached (but not

TEXTBOX 1: KEY COMPONENTS OF STRONG INFERENCE IN SADS

Progress in a scientific field depends on using a successful inferential framework (Platt 1964). Here we highlight six important inferential issues of high relevance to making progress in the study of SADs.

(1) *Competition:* A disappointing number of presentations of new SAD theories make no attempt to even compare how well their predictions fit data in comparison to other theories, thus avoiding even the most basic requirement of Platt's strong inference or Burnham & Anderson's (1998) model comparison approach – a contest among theories. The end result has been a large number of theories that fit reasonably well without a clear sense of how the theories compare with each other. When choosing models to compare against, we strongly recommend including a flexible, simple model like the untruncated lognormal. Comparing against older but less flexible models such as the logseries or geometric which are known to fail to fit many datasets is weaker.

(2) *Multiple mechanisms:* Any given mathematical formulation of an SAD can be created by many different mechanisms, so fit to data cannot possibly be ultimate proof of a particular mechanism (Pielou 1975; McGill 2003a). For example, Cohen (1968) showed that multiple mechanisms lead to the broken stick, Boswell & Patil (1971) showed that multiple mechanisms lead to the logseries while Ugland & Gray (1983) showed that either niche-based competition or neutrality can lead to neutral patterns and processes. It is well known to philosophers of science that similarity in pattern does not imply similarity in process, but ecologists seem to frequently forget it. This fact is clearly demonstrated by the recognition that the SAD shape is an accurate description not only of abundances within a community but of the distribution of incomes among humans, the size of storms, the frequency (abundance) of words in the corpus of Shakespeare's work (Nee 2003) and a host of other distributions (McGill 2003a; Nekola & Brown 2007). Either the mechanisms underlying this one pattern must be extremely diverse or (perhaps and) they must be extremely general and vague along the lines of central limit theorems.

(3) *Decisive weight of evidence:* Most theories produce SADs that are so similar to each other it is difficult to distinguish them given the noisy data and the fact that the differences are most pronounced in the tails which are by definition infrequently observed (McGill 2003a,b; but see Etienne & Olff 2005). Indeed many different SAD theories often fit a single dataset extremely well (McGill 2003a,c) and to single one out as best is to magnify minute differences. Does the mere fact of one theory explaining 99.1% of the variation make it better than the 2nd best theory which explains 99.0%? This may seem like a contrived example but it is quite realistic (McGill 2003c). Wilson (1993) and Wilson *et al.* (1998) found that the noise of sampling effect was so much larger than the small differences that even when the SADs were Monte Carlo generated from known theoretical distributions, the best fit model was usually a different one than the model which generated the data.

(4) *Robust measurement evidence:* Different, inconsistent methods are used. One data set (tropical trees on Barro Colorado Island) has variously been claimed to favour the neutral zero-sum multinomial or lognormal depending on the methods used (McGill 2003c; Volkov *et al.* 2003). The outcome in this particular case and in general is heavily dependent on the measure of goodness of fit used (McGill 2003c; Magurran 2004; McGill *et al.* 2006b). Unfortunately different goodness of fit measures all emphasize different aspects of fit (chi-square on log-binned data emphasizes fitting rare species, calculating an r^2 on the predicted vs. empirical CDF emphasizes the abundances with the most species - usually intermediate abundances, while likelihood emphasizes avoidance of extreme outliers, etc.). It is common for different measures of fit to select different SAD theories as providing the best fit to a single data set (McGill 2003a). Thus any claim of a superior fit must be robust by being superior on multiple measures.

(5) *General across multiple data sets:* Even when consistent methods are used, most theories will fit some datasets well and other datasets poorly. Within the basic hollow curve form there is great natural variability in empirically observed shape (especially for log-abundances) so it is almost always possible to find a dataset for which a theory works and a dataset for which it fails. One interpretation is that different mechanisms are operating in different communities and indeed this might be true for fishes vs. trees (Etienne & Olff 2005). But is it really parsimonious to believe that different processes govern bird communities on different Breeding Bird Survey routes within the same habitat type (McGill 2003a) or tropical trees on Barro Colorado island vs. Pasoh forest (Volkov *et al.* 2003) based solely on extremely small differences in the goodness of fit of two different SAD theories?

about mechanism – point 2). But every study of which we are aware that meets all (or even two) of these criteria has found that no one SAD is superior (Wilson 1991; Wilson et al. 1996; McGill 2003a; Volkov et al. 2003; Etienne & Olff 2005). We do not believe that examining small variations in the nature of the hollow curve will ever lead to strong inference and decisive tests of SAD theories.

Integrating SADs with other patterns – towards a unified theory?

One positive theoretical development in the study of SADs is the demonstration that SADs are intimately linked in a mathematical sense with a wide variety of other well-known and novel macroecological patterns. This begins to approach the rather grandiose goal of 'unified theories' (Hanski & Gyllenberg 1997; Hubbell 2001; McGill 2003a; Harte et al. 2005). These linkages can go in one of two directions:

(a) One can start with only a hollow-curve SAD and then derive other macroecological patterns from it, or.

(b) One can start with some set of assumptions and then derive many macroecological patterns (including SADs) from these assumptions.

Type (a) approaches are essentially elaborations of the consequences of sampling from an uneven, hollow curve SAD (see Textbox 2). Although many find this biologically uninteresting, it is important to identify just how much is explained by sampling from the hollow curve of the SAD alone. For example, few people realize that Preston (1960) showed that most of the species area relationship was well explained by sampling from the logseries up to fairly large spatial scales. From a testing point of view, it is also important to realize that testing a prediction based on sampling from an SAD (such as the species area curve discussed in Textbox 2) is not really an independent prediction from the hollow curve SAD prediction.

TEXTBOX 2: SADS – THE MASTER PATTERN?

If one starts with an SAD as the description of the relative abundances of species in a community, one can start sampling individuals from the SAD representation of the community and derive a number of patterns. This makes the SAD a central pattern in developing a unified theory that links patterns together. Most directly, the species-individual curve (SIC) which plots number of species as a function of the number of individuals sampled follows immediately. This curve is also known as a collector's curve (Coleman 1981), a species accumulation curve (Ugland et al. 2003) or a rarefaction curve (Sanders 1968). The exact species-individual curve derived depends on the exact SAD. For example, the logseries produces the exact relation $S = \alpha \ln(1 + N/\alpha)$ (Preston 1960; Williams 1964), neutral theory produces an alternative, more complex formula (Etienne & Alonso 2005) while May (1975) derived sampling formulas for several other SADs. The analytical form of the SIC given an empirical SAD (i.e. a sample with abundances of the different species measured) is also well worked out (Simberloff 1972; Heck et al. 1975; Olszewski 2004). It was recently shown (Olszewski 2004) that the initial slope of the SIC is equal to a common measure of community evenness, Hurlbert's (1971) probability of interspecific encounter which is, in turn, a bias-corrected form of Simpson's diversity index. Preston (1960) showed how the z-value of the species area relationship (SAR) is entirely explained by passive sampling from a logseries SAD at small scales with another factor (presumably habitat heterogeneity) starting to play a role only at larger scales (see also Williams 1964;

Rosindell & Cornell 2007). The SIC curve is often conflated with a species area curve, but this is a good equation only if the system is spatially homogeneous and well-mixed. If dispersal limitation or environmental heterogeneity exist, or equivalently there is spatial autocorrelation or non-Poisson distribution of individuals then the SAR curve will deviate from the SIC (Gotelli & Colwell 2001; Olszewski 2004). He & Legendre (2002) systematically explored how the SAR changes depending on the degree of aggregation of individuals within species.

The pattern of nestedness (Atmar & Patterson 1993; Wright et al. 1998), wherein the species occurring on small patches are a proper subset of the species occurring on larger patches can also be created entirely by a passive sampling process from a hollow curve SAD – the species found on all patches are the abundant species while the species found only on the large patches are the rare species (Connor & McCoy 1979; Fischer & Lindenmayer 2002). Similarly, sampling from an SAD can explain the link between abundance and occupancy (Maurer 1990; Lawton 1993; Gaston 1996; Gaston et al. 2000), leading in turn to the derivation of the distribution of occupancies (and hence range sizes by some definitions) from SADs. Incidence curves (Hanski & Gyllenberg 1997) also can be derived from passive sampling. These various links to SADs can also be combined. For example, better species accumulation (and species area) curves can be achieved by taking the abundance/occupancy relationship into account (He et al. 2002; Ugland et al. 2003). As with the SAR, factors other than sampling from SADs may also affect nestedness and abundance-occupancy, but these are not yet well understood.

Type (b) approaches (the realization that a small set of assumptions can simultaneously produce hollow curve SADs and other macroecological patterns) are even more recent and, we believe, promising. The most prominent such example is neutral theory (Caswell 1976; Bell 2000, 2003; Hubbell 2001; Chave 2004), which can derive a great many predictions including SADs but also the variability over time of species abundances and true species area curves (Rosindell & Cornell 2007) which incorporate the role of dispersal limitation. To neutral theory's great credit, this is one reason it has been falsifiable (Dornelas *et al.* 2006; McGill *et al.* 2006b). In contrast most SAD models such as the statistical and the niche partitioning models make no prediction other than the hollow-curve SAD (but see Ugland *et al.* 2007). This elegant ability of neutral theory to produce many predictions is probably the main reason for the interest and attention it has inspired (Alonso *et al.* 2006).

Another body of work that has received less attention but which can also derive many predictions focuses on the spatial organization of individuals. An SAD is just a collection of individuals in an area. If we can describe the spatial distribution of individuals, then we can predict the nature of the SAD for a given area using patterns (spatial distribution) that may be closer to certain important mechanisms such as dispersal and environmental heterogeneity. Empirically, we know the spatial distribution of individuals within a species tends to be clumped (aggregated; Condit *et al.* 2000) while the distribution between species tends to be independent (spatial Poisson randomness; Hoagland & Collins 1997). Such distributions have been studied at two very different scales. At very large scales, this clumping has been described as an abundance surface with an approximately Gaussian-bell curve shape (Whittaker 1967; Brown *et al.* 1995), which leads to a model producing a number of macroecological predictions (Gauch & Whittaker 1972; Hengeveld *et al.* 1979; McGill & Collins 2003). At smaller spatial scales the clumping of individuals can be modelled based on fractals (Harte *et al.* 1999), statistical mechanics (Harte *et al.* 2005), or Ripley's K-statistic (Plotkin & Muller-Landau 2002). At any scale the two assumptions of independence between species and aggregation within species lead to predictions about SADs as well as a variety of other macroecological patterns (Gauch & Whittaker 1972; Hengeveld & Haeck 1981; McGill & Collins 2003; Harte *et al.* 2005). Such spatial distribution models have also tended to lend themselves well to empirical tests (Green *et al.* 2003; McGill & Collins 2003) .

In summary, there has been a proliferation of models purporting to explain hollow-curve SADs. The vast majority only predict the existence of a hollow-curve SAD, making them essentially untestable. More recently, multifaceted theories that link SADs with other patterns have emerged and proven more amenable to testing.

EMPIRICAL DEVELOPMENT OF SADS

A healthy scientific discipline has theoretical development and empirical discovery proceeding hand-in-hand. We suggest that on the whole there has been more theoretical development of SADs (Table 2) than empirical development (or at least that theory has received more attention). However, a great deal of interesting work has also occurred in exploring empirical patterns of SADs. We will first summarize the classical work on SADs found in ecology textbooks, and then review a series of less-well-known, intriguing but not strongly documented empirical results.

Classical empirical work

The bulk of the empirical work (and again the work put into textbooks) has established two facts: (i) SADs follow a hollow curve (on arithmetic scale) in every system studied and (ii) Within this broad constraint, there is a great deal of variation in the details, especially as highlighted on a log-scale. We cannot possibly list every empirical measurement of SADs as this is one of the most common types of data collected in ecology. And in all likelihood, the majority of such data sets have never even been published (e.g. collected for management or monitoring purposes). Hughes (1986) gives a compilation of 222 different SADs and Dewdney (2000) gives a compilation of 100. To our knowledge no SAD ever measured violates the basic hollow-curve shape on an arithmetic scale, justifying the claim that it is a universal law. As with any pattern, it is possible that more work will uncover an exception. For example, our knowledge of the shape of SADs amongst taxa such as bacteria or mycorrhizae is poor. But there is no debating that the hollow-curve SAD is unusually general in nature.

At the same time enormous debate has gone into the nature of the left side of SADs when plotted on a log-abundance scale (Preston 1948; Hughes 1986; Southwood 1996; Hubbell 2001; McGill 2003b). Ecologists have observed patterns ranging from a histogram that increases to a mode in the middle (e.g. Fig. 2a BCI, BBS) through to data that is largely flat until the middle abundances (e.g. Fig. 2a Bass Strait) then on to data that has its mode at the lowest abundance of $N = 1$ and decreases continuously from there (e.g. Fig. 2a NCS). This goes back to the earliest days, with Fisher suggesting that a lognormal was impossible as his insect data showed the mode at the lowest abundance. Preston explained this with the concept of a veil line (Preston 1948). Preston's veil line suggests that small samples do not capture the truly rare species which causes
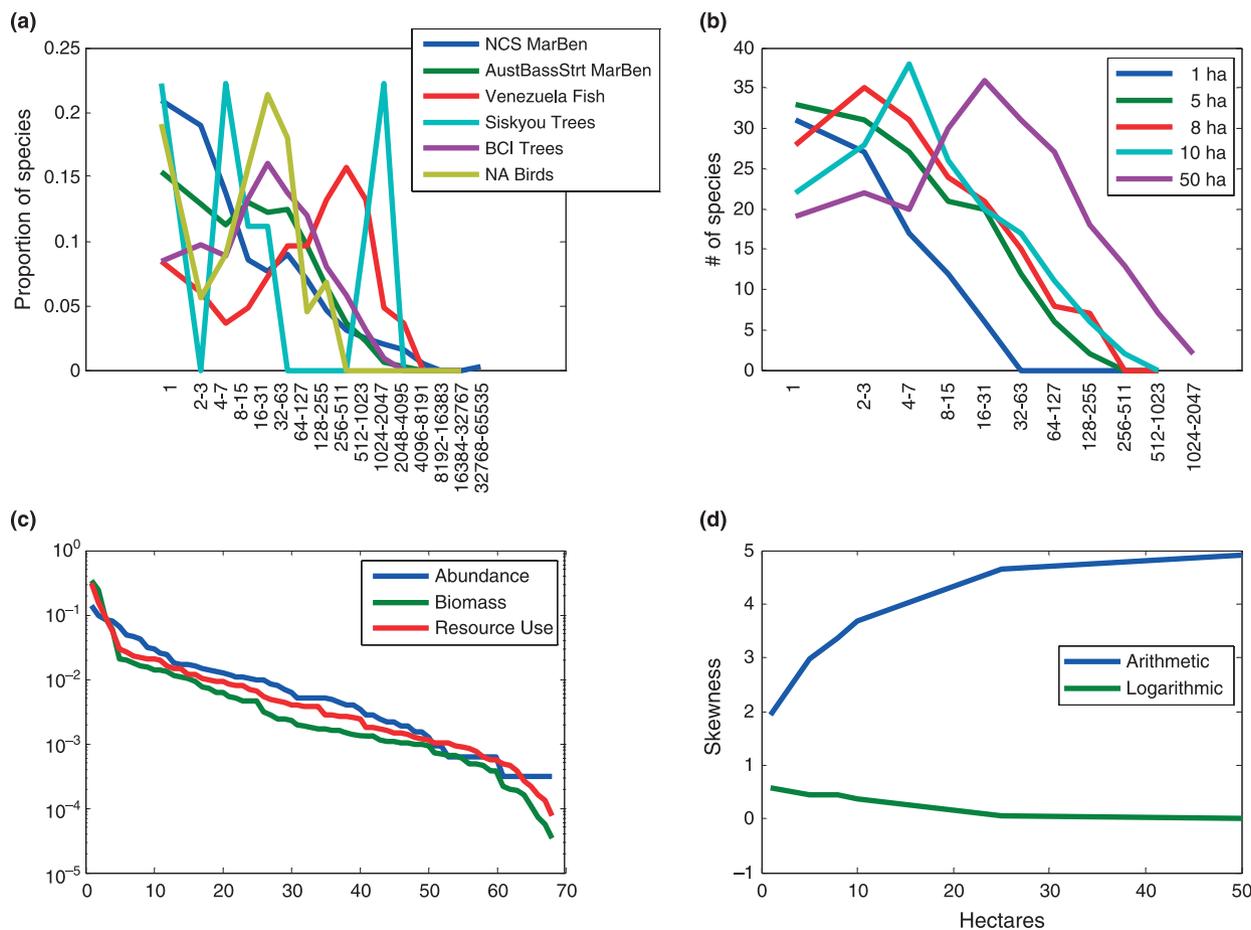
Figure 2 Display of various empirical patterns discussed in the main text. (a) Plots on a log-abundance scale of six different datasets (with species richness, S, and number of individuals, N given): NCS marine benthic macrofauna ($S = 458$, $N = 102,926$: personal communication John Gray and Karl Ugland), Australian Bass Strait marine benthic macrofauna ($S = 801$, $N = 60,391$: personal communication John Gray and Karl Ugland), fish in an estuary in Venezuela ($S = 83$, $N = 28,975$: Winemiller 1990), temperate trees of the Siskyou mountains ($S = 9$, $N = 3,342$: Whittaker 1960), Tropical trees of Barro Colorado Island (BCI) ($S = 225$, $N = 21,457$: Condit *et al.* 1996) and route from the North American Breeding Bird Survey (BBS) ($S = 89$, $N = 2,783$: Robbins *et al.* 1986). The *x*-axis is log 2 bins. The *y*-axis is percent of species within the community; this rescaling was performed for allowing easy comparison between SADs. This data are normally plotted as a bar chart (e.g. Fig. 1b), however, lines are used here to make it easier to track the six different SADs. (b) An example of unveiling. The SAD for progressively larger areas of the 50 ha BCI tree data are plotted. (c) An example of how an SAD changes with different currencies, here taken from the NA Breeding Bird Survey. Again the *y*-axis is a log percentage of total currency (e.g. biomass) in the community to allow for comparisons. (d) An example of how basic descriptors of an SAD (skew on arithmetic and log scales) change with scale drawn again from the 50 ha BCI tropical tree data.

the left side of the SAD to be truncated behind a veil resulting in a mode at $N = 1$. The veil line gradually disappears with increased sampling (Fig. 2b; reviewed in Marquet *et al.* 2003). But later authors have argued that the mode remains at $N = 1$ no matter the extent of the sampling (Hughes 1986; Southwood 1996; see also Fig. 2a NCS or Bass Strait). Whittaker (1965) attempted to resolve this debate by suggesting that no one curve fit all data – the geometric model applied to species poor communities while the lognormal applied to more species rich communities, only being fully unveiled in large samples. As already

discussed, this classical empirical work has not proven sufficient to differentiate among various mechanistic models, even with variation in the left tail on a log scale. This is in part because the patterns are inconsistent in this regard (perhaps because the role of sampling effects have not been well worked out to distinguish between empirical pattern vs. sampling), and in part because the difference is just too subtle to give a decisive test. In the rest of this section we identify eight alternative, less well-known empirical patterns which might lead to decisive tests. All of these patterns need much more work to assess their generality.

Empirical pattern 1 – environmental gradient analysis

Community ecology is regaining interest in the environmental (abiotic) context in which communities occur. In particular, gradients of changing environment provide a natural experiment or comparative basis for testing theories about communities (McGill *et al.* 2006a) including SADs. The 1970s saw a burst of analysis of SADs along gradients. Fig. 1d gives an example; the data in Fig. 1d is from Whittaker (1960) (inspired by a comparable plot with different data in Whittaker 1965) that plots changes in SADs along elevational gradients in productivity. Whittaker interpreted the results as showing that low productivity systems have extremely uneven SADs and are well fit by a geometric SAD, while high productivity systems are well fit by lognormal curves (and show the highest evenness). Later, Whittaker (1975) repeated this analysis with a similar outcome, but with the unique twist that he compared vastly different communities (birds, trees, etc.). He thereby illustrated one of our aforementioned advantages of SADs – the ability to compare unrelated communities. Hubbell (1979) likewise showed a similar plot along a latitudinal productivity gradient, comparing different tree communities ranging from boreal to tropical (again with little overlap in species between communities compared). Thus a general pattern of increasing evenness (more lognormal, less geometric) with productivity was suggested. Unfortunately, to our knowledge, this pattern seems to have had little follow-up. It is also unclear how much this pattern was driven solely by the change in species richness which has a strong effect on the shape of RADs; better analytical methods are needed. One study that did control for species richness (Hurlbert 2004) confirmed that sites with greater productivity had more species for a given number of individuals and less dominance by the most abundant species, indicating a positive productivity-evenness relationship. Cotgreave & Harvey (1994) showed that more complex habitats (often correlated with productivity) showed SADs with higher evenness (they also showed that communities with more similar body sizes showed less evenness, suggesting a mechanism of competitive overlap affecting SADs). Although the pattern of greater evenness in high productivity environments is far from well documented, evidence to date is consistent; but we know of not even one instance where a model for SADs attempted to explain the change of SADs with productivity.

In the 1970s, marine ecologists began to explore whether SADs might prove to be a good indicator of human-disturbed (specifically polluted) environments. One of the first such analyses (Gray 1979) explored various pollution factors such as organic waste, oil and toxic industrial efflux and found a decrease in rare species and an increase in species of intermediate-abundance. Amazingly, of the 138 papers (as of March 2007) that cite this original work, one is fresh water, six are terrestrial (mostly theoretical), and the remaining 131 are all marine. Despite evidence that SAD responses to human disturbance in marine systems apply equally well to terrestrial taxa (Hill *et al.* 1995; Hamer *et al.* 1997) this tool remains almost unknown amongst terrestrial practitioners, although Mouillot & Lepretre (2000) have also found that SADs perform well in distinguishing terrestrial communities under different influences and argue for their use as indicators. The marine community has developed a variety of elaborations on this basic idea such as k-dominance plots (Patil & Taillie 1982; Lambshead *et al.* 1983) and abundance/biomass comparison (ABC) plots (Warwick 1986; Clarke & Warwick 2001; Magurran 2004). It seems that SADs have a high potential to serve as environmental indicators, defined as an easily measured index that is indicative of the state ('health') of an ecosystem (Bakkes 1994). While conservation uses indicators extensively, the main challenge is to find ones that are easy to measure but highly informative and usable with non-technical audiences. SADs, which come from easily measured data and are intermediate in complexity, may have tremendous potential.

Empirical pattern 2 – successional and other temporal gradients

Instead of comparing communities across space (gradients) it is also possible to compare communities across time (Magurran 2007). Bazzaz (1975) showed a series of SADs along a successional gradient in old fields (with more lognormal, more even communities occurring late in succession just as for productivity). Caswell (1976) studied changes in diversity over succession and found that his version of neutral theory failed to produce empirically observed patterns. This allowed Caswell to make a strong (Plattian) inference about an SAD theory, supporting our contention that this comparative approach holds promise. Wilson *et al.* (1996) demonstrated fairly complex but significant changes in which SAD fits the best over succession in several grasslands, with evenness increasing. Thibault *et al.* (2004) showed a significant directional change in the shape of SADs over a 25 year period in a system which was known to have experienced a strong climatic trend (increased rainfall in their arid system).

Empirical pattern 3 – deconstruction or subsetting

Rather than comparing SADs from two communities, one can compare SADs for two subsets within the same community. This approach has been coined deconstruction (Marquet *et al.* 2004). For example Labra *et al.* (2005) studied a set of invasive bird species vs. a paired set of similar native

species and a random (unpaired) set of native species and found that exotics showed a clear tendency towards higher abundances, especially in the rare species (although they pooled data from many sites making it not strictly an SAD). The division of species into resident and transient also shows very distinct differences in the shape of the SAD (Magurran & Henderson 2003; Ulrich & Ollik 2004). On the theoretical modelling side, a somewhat similar idea was suggested by Etienne & Olff (2004a) who explored constraints based on body mass between body size guilds, but assumed neutrality within body size guilds. We know of few other analyses, but imagine that deconstructions comparing the SADs of species from different trophic levels (e.g. predator vs. prey), ontogenetic stages (juvenile vs. adult) or taxonomic groups (e.g. passerines vs. non-passerines) might also prove interesting.

Empirical pattern 4 – transient species, scale and left-skew

Recent years have seen a rapid advance in understanding what drives the shape of the left tail on a log scale, and in particular the common observation that large scale data sets are left-skewed (have more rare species). Gregory (2000) showed that left skew on a log scale is common in large (country-sized) assemblages of birds, but that it disappears when species arguably not part of the community are removed. Magurran & Henderson (2003) showed that amongst fish in an estuary, the permanently resident species were lognormal (with no excess of rare species), but the transient species were logseries indicating a disproportionate number of rare species. A similar result was obtained for beetles (Ulrich & Ollik 2004). McGill (2003b) explored this same idea in the context of autocorrelation. He showed low autocorrelation (all transients) and high autocorrelation (few transients) leads to zero skew, while intermediate autocorrelation (mixture of residents and transients) leads to log-left-skew (excess rare species) in both Monte Carlo models and empirical data (see also Fig. 2d). Finally, neutral theory (Hubbell 2001) predicts that higher rates of migration, modelled by the parameter m, lead to more log-left skew. Although immigration rates *per se* are hard to measure, several authors (Hubbell 2001; Latimer *et al.* 2005) have fit empirical data to the neutral theory and found more left-skew (i.e. higher values of m) in cases where greater immigration was expected. These independently developed but intertwined lines of evidence point both empirically and theoretically to the idea that communities more open to immigration will have a higher proportion of rare species.

Empirical pattern 5 – multiple modes

It has occasionally been observed that SADs of large assemblages appear to be multimodal, that is have more than

one peak in a histogram (Ugland & Gray 1982; Gray *et al.* 2005; see also Fig. 2a NA BBS Birds and Venezuelan Fish). This is in contrast to most theories which have only a single peak either at intermediate abundances (e.g. the lognormal) or at $N = 1$ (e.g. logseries). Sampling noise and binning effects can produce multiple peaks (as in Fig. 1a), but only small ones, while peaks much larger than could be produced by these effects are claimed to be observed. Preston's method of displaying SAD histograms on a $\log_2$ scale by dividing the boundaries (1, 2, 4, etc) between adjacent bars has the effect of smoothing out peaks that might actually occur at $N = 1$ or $N = 2$ thereby hiding the potential for multiple peaks (Gray *et al.* 2006). The existence and implications of multiple modes in the SAD has been little explored. An analysis of 100 Breeding Bird Survey routes found that all 100 routes had a peak at $N = 1$ or 2 and a second peak at higher numbers (McGill unpublished data). One can use a finite mixture of normal distributions on a log scale fit by expectation maximization (MacLachlan & Peel 2000; Martinez & Martinez 2002) combined with AIC or likelihood ratios to test for the number of peaks. Using these methods, McGill (unpublished data) analysed the 50 ha tropical tree plot at Barro Colorado Island and found that AIC selected a model with three peaks, just as predicted by Gray *et al.* (2005). In the strongest evidence to date, Dornelas *et al.* (in preparation) not only found multiple peaks but found that these peaks are consistent as sample size increases (the peaks move to the right as expected when sample size increases but the distance between the peaks remains constant).

The exact number of peaks chosen will depend on one's personal preference in tradeoffs for parsimony vs. goodness of fit (or the information criteria one chooses that makes these tradeoffs for you). The fact that there is more than one peak in the data for many communities suggests there is much to be gleaned by documenting, testing, and explaining this pattern. While the existence of multiple peaks on a log scale does not reject the universal hollow curve law on an arithmetic scale, it does reject every existing SAD theory which all produce unimodal curves. One possibility is that these studies inappropriately lumped together distinct guilds. If true then deconstruction analysis might find appropriate separations (Magurran & Henderson 2003; Marquet *et al.* 2004).

Empirical pattern 6 – High and low diversity systems

The vast majority of SADs have been studied in systems with a moderate number of species (say 30–300). Recent debate over SADs has relied extensively on a single data set: the approximately 225 species, 50 ha tropical tree plot from Barro Colorado Island. Yet patterns from extremely species poor and extremely species rich systems do not necessarily match generalizations derived from systems of intermediate richness. For example, large swaths of boreal forest may

contain only half a dozen tree species. It is tempting to ignore such systems as uninteresting, but they of course represent large areas of the world's surface and are of considerable economic importance. Boreal forest SADs tend to produce histograms that are quite flat (non-modal) on a log-abundance histogram (or equivalently a straight line on a RAD; e.g. see Fig. 2a Siskiyou trees). These can be fit by the geometric model (Motomura 1932). Models of SADs generated by neutral theory or the lognormal actually fit such data very poorly. Moreover, it is not uncommon in few-species SADs for the two most abundant species to be very similar in abundance (i.e. codominants; see the 1920–2140 m band in Fig. 1e), which contradicts the geometric model. At the other extreme, extraordinarily speciose communities (100s of species amongst a few 1000s of individuals) tend to produce an SAD that still looks hyperbolic on a log-abundance scale (e.g. Fig. 2a NCS), again fitting SAD models other than the logseries quite poorly.

Empirical pattern 7 – measurement currencies other than abundance

Ecologists have a long tradition of plotting histograms of abundance, but plant ecologists sometimes use other measures (e.g. percent cover) for reasons of convenience and preference. It seems desirable to explore the implications of using different currencies to assess the importance of a species (Tokeshi 1993; see Fig. 2c). Abundance is clearly an important measure, but perhaps biomass, resource use (roughly biomass to the ¾ power; Savage *et al.* 2004) or percent cover is more relevant (Chiarucci *et al.* 1999). More importantly, perhaps one of these distributions can lead more directly to a mechanistic theory. In particular, niche partitioning models might be expected to more directly explain resource use than abundance (Tokeshi 1993; Thibault *et al.* 2004; Connolly *et al.* 2005; Ginzburg personal communication). Ecologists studying marine systems have long used differences in biomass and abundance plotted together in curves called Abundance Biomass Comparisons (ABC curves; Warwick 1986) as a diagnostic tool. Connolly *et al.* (2005) showed that the effects of scale and the rate of unveiling differ substantially between abundance and biomass distributions. Thibault *et al.* (2004) also found that the two curves showed very distinct patterns.

Empirical pattern 8 – Patterns based on 'labelled' SADs

Our definition of SADs requires that the SAD be 'unlabelled', but as we seek to advance our empirical understanding of the patterns related to SADs, comparing the abundance of individual species over time or space is an obvious direction to turn (Dornelas *et al.* 2006; Etienne

2007). For example, how often does a rare species become common or a common species become rare? Some theories (Hanski 1982) predict fairly quick exchanges, others (Hubbell 2001) predict fairly moderate rates of change, while empirical data suggest that species retain their basic status as common or rare up to one million years (McGill *et al.* 2005). Wootton (2005) was able to reject a particular SAD theory by experimentally removing the dominant species and showing that the abundances of the remaining species changed more than expected under neutral theory. A similar result was obtained for fragmented tropical rainforests (Gilbert *et al.* 2006). Mac Nally (2007) also shows greater difference in labelled than unlabelled studies and introduces the 'abundance spectrum' as a means of studying changes in labelled SADs. Murray *et al.* (1999) has shown the potential of comparing labelled SADS between sites.

A theory which not only predicts a hollow curve SAD but predicts which species (or types of species) should be abundant or rare would be extremely powerful. There has been a great deal of speculation about which species should be abundant (e.g. Rosenzweig & Lomolino 1997), but there has been comparatively little success to date in the empirical search for patterns (Murray *et al.* 1999, 2002). For example, more common species tend to have smaller body size (Damuth 1981, 1991; Marquet *et al.* 1990; White *et al.* 2007) but the exact nature and strength of the relationship is still debated (Russo *et al.* 2003; White *et al.* 2007). Careful control for spatial variation and phylogeny may lead to clearer results (Murray & Westoby 2000). Perhaps this is an area where theory can produce new predictions to guide empirical research. Recent work centred on traits may provide such a solution (Shipley *et al.* 2006).

Finally, with labelled species we can look at questions related to the phylogenetic context of the SAD (Webb *et al.* 2002). For example, how do the abundances of sister species compare? A study by Sugihara *et al.* (2003) suggests that sympatric, closely related species have reduced abundances, presumably because of competition for more similar resources than non-sister pairs.

In summary the classical empirical work on SADs clearly established that the hollow-curve SAD is very general, but that when placed on a log scale that magnifies the rarest species considerable variation occurs. The classical work has failed to strongly test and reject different mechanistic theories. We identify eight patterns involving comparison of SAD shape between communities or subsets of communities (pattern nos. 1–4), seeming exceptions (pattern nos. 5–6) and alternative views of SADs (pattern nos. 7–8) that have promise for leading to stronger tests of mechanistic models. Note that even the seeming exceptions (no. 5 and 6) occur only on log-scales and do not violate the hollow-curve rule on an arithmetic scale.

LINKING THEORY AND DATA – STATISTICAL ISSUES IN SADS

Data and theory are tied together through a process of measurement and quantification. In the case of SADs a variety of statistical issues arise that may substantially affect the appearance of the observed patterns and should be resolved to ensure a tie between data and theory in which we can have confidence. We identify four broad areas.

How does sampling affect the shape of SADs?

Every SAD is a finite sample, yet we know very little about how much this affects the patterns we observe. Sampling leads to variance. Variance means that SADs have error bars around the curves that represent them. In a plot such as Fig. 1d the lines appear distinct but it is hard to say without error bars. We know little about how to place error bars and do significance tests on SADs, and it is rarely performed. Neutral theory has a sampling theory built in (Etienne 2005; Etienne & Alonso 2005; Alonso et al. 2006), which is a tremendous advantage, but this needs to be extended to SADs more generally. Some basic machinery has been developed (Pielou 1977; Dewdney 1998; McGill 2003b; Green and Plotkin 2007), but much work remains. Munoz et al. (in press) have shown that not only the variance but the bias of neutral parameters derived from SADs can be extremely high even when sample sizes are moderate (100s of individuals; but see Etienne 2007). We cannot currently answer several closely related basic questions of high practical importance: what number of individuals/proportion of individuals in a community/spatial extent do we need to sample to have reasonable confidence that the SAD obtained is a good approximation of the underlying community? Is 1% of the individuals enough? or 1000 total individuals?

How does scale affect the SAD?

Closely related to the question of sample size is the question of scale. As one samples larger areas or for longer time periods, the sample size increases, and issues of habitat heterogeneity, β-diversity, clumping of individuals, and autocorrelation must be addressed. It is entirely possible that both the patterns and processes influencing the SAD will change with scale (Wiens 1989; Levin 1992) as has been found for other macroecological patterns (Rosenzweig 1995). For example, it has been the suggested that the shape of an SAD changes with log left (negative) skew increasing with scale possibly due to spatial autocorrelation (McGill 2003b; see Fig. 2d). Is there, then, a natural or optimal scale at which to measure SADs? This returns to our original definition of the SAD and the imprecision that is inherent in

measuring a poorly defined concept like 'community'. Some of the aforementioned links between SADs and other macroecological theories may prove important.

How do we compare SADs?

Nearly all comparisons of SADs along gradients, deconstructions or time trajectories to date have been purely by visual inspection (Whittaker 1965; Hubbell 1979). Most particularly, these visual inspections have been performed on rank-abundance plots which, by using an x-axis that runs from 1 to S (i.e. species richness), seriously confounds the effects of species richness per se with other changes in the shape of the SAD (e.g. lines appear quite distinct in Fig. 1d but less so in Fig. 1f). Changes in species richness are a legitimate factor that should be considered a change in shape of the SAD. However, changes in richness so strongly dominate in rank-abundance plots that no other changes are easily considered. Is there any other change in the shape of an SAD after controlling for the fact that productivity affects richness? We cannot say at the present time (but see Hurlbert 2004). It may be that the use of empirical cumulative density function (ECDF) plots can remove some of this bias (Fig. 1f). The analyses of human impact in marine environments usually use such plots (Gray 1979) or k-dominance plots (Lambshead et al. 1983) which are another way to try to remove the effect of species richness. Plots that use relative abundance (percent) of individuals or percent of total species may help. Such methods represent an improvement, but are still visual. More rigorous multivariate methods are needed.

What kinds of variation are commonly found in SADs and how are they related to each other?

We know almost nothing about the main axes of variation in SADs. In morphometric analyses it is common to perform some form of principal components analysis and have a few orthogonal axes capture most of the variation. A similar result has occurred in landscape ecology where over four dozen landscape metrics were found to reduce to only six distinct axes of variation (Riitters et al. 1995) capturing 87% of the total variation. This needs to be performed for SADs. Species richness, evenness and proportion of rare species might well turn out to be distinct axes of variation, but at the same time these factors may be correlated with each other. Empirical results to date are mixed (Kempton & Taylor 1974; Weiher & Keddy 1999; Stirling & Wilsey 2001; Wilsey et al. 2005). What are the optimal indices that capture the major axes of variation in SADs? We do not know. Two recent developments are promising. The observation (Pueyo 2006) that the power distribution, logseries and lognormal are all just successive terms in a Taylor series expansion

suggests that we may be able to develop a rigorous framework for how flexible an SAD is needed in a particular case (as well as giving some credence to the parameters of these distributions as possibly being more general in interpretation than currently believed). Secondly, a new model, the gamma-binomial or gambin (Ugland *et al.* 2007), seems to be able to fit a great many datasets well while having only a single parameter that seems to do a good job of discriminating along gradients.

GOING FORWARD

Like any field, the study of SADs has had successes and failures. A major success is the frequent measurement of SADs in a wide variety of taxa and geographic areas leading to the establishment of the relative universality of the hollow-curve SAD law. Another major success is uncovering a variety of tantalizing possible empirical patterns that go beyond the hollow-curve. A final success is that the SAD has inspired a great deal of theoretical development in community ecology. Against these successes must be weighed several failures. These include not firmly establishing any empirical patterns beyond the hollow curve and a failure to develop tools to differentiate how much of the patterns are due to sampling effects vs. other more ecologically based effects. Probably the biggest shortcoming to date has been the lack of strong inference wherein an extreme proliferation of mechanistic models remains largely untested.

How can we bring strong inference into the field of SADs? Platt (1964) not only argues that we must bring theories into competition with each other, which has happened often enough in the study of SADs (Wilson 1991; Wilson *et al.* 1996; Etienne & Olff 2005), but the theories must make distinct enough predictions that we can have a decisive test. Similarly, Lakatos (1978) suggests that it is the quality and novelty of predictions that make for a successful research program. How do we move SAD research to novel predictions leading to decisive tests?

We suggest that SADs, like most of ecology, will never find the kinds of predictions that physics makes and which Lakatos praised (such as the prediction of the existence of Neptune from small perturbations in the position of Uranus). Ecology does not make predictions that are accurate to five decimal places like physics does. Instead, Rosenzweig & Abramsky (1997) argues that not just SAD theory but all of ecology does and should proceed by 'dipswitch testing' (for younger readers, a dipswitch is an approximately 1 cm by 2 cm switching unit that contains usually eight on/off switches on a printed circuit board that used to be the main way to configure a computer). What ecology does well is to make a lot of binary predictions (*y* increases when *x* increases). A single binary prediction

that is empirically confirmed is weak evidence for a theory (*a priori* 50/50 odds). But if, like a dipswitch, we have enough binary predictions strung together, then it creates a strong test that is achievable in ecology. This of course assumes that the model making these multiple predictions is parsimonious and not over-parameterized.

So where does the dipswitch of multiple predictions emerge in the study of SADs? We believe that SADs are a central pattern but cannot be an isolated pattern. We have argued the greatest failing in the study of SADs is the development of theories that make only a single prediction – the hollow-curve shape. We advocate placing SADs into a larger ecological context, such as the abiotic environment, the trophic level in a food web, or the status as invasive species. This will lead to many predictions resulting in stronger testing and simultaneously demonstrate exactly how centrally SADs are embedded in ecology as a whole. These more integrated SADs are much more likely to increase our understanding of the mechanisms that lead to hollow-curve SADs. In a sign of the strength of these more integrated approaches, it is possible to imagine controlled, manipulative experiments (field or microcosm) that test such integrated theories; heretofore SADs have depended entirely on observational data. These ideas of integration have been the main themes identified throughout the theoretical, empirical and statistical sections of this review. We summarize them into a top dozen list of future directions for going forward in the study of SADs (Textbox 3).

We are optimistic that the SAD will, in the long run, prove to be one of the most important fundamental tools in community ecology and management. But to get there we must always think carefully about Platt's model of strong inference. We hope our proposed directions forward based on producing more predictions by integrating SADs into their ecological context and the many examples we gave of work already following this direction will prove a catalyst. Then maybe we will begin to answer the big questions in SADs such as why are all SADs broadly similar (hollow curve), where (and why) do predictable differences in the finer-scale structure of SADs occur, and how might we best quantify these differences?

ACKNOWLEDGEMENTS

TEXTBOX 3: TOP DOZEN DIRECTIONS TO PURSUE IN SAD RESEARCH

For theoreticians:

(1) Produce theories that make *many predictions simultaneously*, of which a hollow curve SAD is only one.

(2) Produce theories that attempt to *predict some of the patterns identified* in our empirical section.

(3) Produce theories that *incorporate questions about sampling and scale* discussed in our statistics section.

(4) Explore exactly how much of and *how many macroecological patterns can be explained* merely as a result of sampling from a hollow-curve SAD.

(5) Test theories against *other theories* using *multiple datasets* using *multiple measures* of goodness of fit.

For field ecologists:

(6) Collect additional data to *confirm the patterns* we suggest might be general in our empirical section. In particular collect data that is anchored in an ecological context and along some axis of variation (e.g. along gradients or containing deconstructable sets such as data that spans across trophic levels).

(7) Collect SAD data in *underrepresented systems* such as bacteria and extremely high or low diversity systems.

(8) Collect as *large a sample size as possible*. As described, we do not know what a good sample size is, but it clearly at least in the 100s and quite possibly in the 1000s of individuals. Similarly, clearly describe the sample size, area and temporal duration of the sample to make the data useful to others.

(9) Collect data using *currencies in addition to abundance* such as biomass or resource use.

(10) Explore *manipulative experiments* (field and microcosm) to test theories of SADs.

For statisticians:

(11) Develop a *sampling theory* of SADs to help understand what variation is explainable by sampling. Extend this theory to cover the effects of scale (essentially autocorrelated sampling).

(12) Use multivariate statistics to develop a robust theory of *comparing SADs* and identify the major independent axes of variation in SADs.

REFERENCES

Alonso, D., Etienne, R.S. & McKane, A.J. (2006). The merits of neutral theory. *Trends Ecol. Evol.*, 21, 451–457.

Atmar, W. & Patterson, B.D. (1993). The measure of order and disorder in the distribution of species in fragmented habitat. *Oecologia*, 96, 373–382.

Bakkes, J.A. (1994). *An Overview of Environmental Indicators: State of the art and Perspectives*. UNEP/Earthprint, Bilthaven, Netherlands.

Bazzaz, F.A. (1975). Plant species diversity in old-field successional ecosystems in southern Illinois. *Ecology*, 56, 485–488.

Bell, G. (2000). The distribution of abundance in neutral communities. *Am. Nat.*, 155, 606–617.

Bell, G. (2001). Neutral macroecology. *Science*, 293, 2413–2418.

Bell, G. (2003). The interpretation of biological surveys. *Proc. R Soc. Lond. B*, 270, 2531–2542.

Borda-de-Agua, L., Hubbell, S.P. & McAllister, M. (2002). Species-area curves, diversity indices, and species abundance distributions: A multifractal analysis. *Am. Nat.*, 159, 138–155.

Boswell, M.T. & Patil, G.P. (1971). Chance mechanisms generating the logarithmic series distribution used in the analysis of number of species and individuals. In: *Statistical Ecology, Volume I, Spatial Patterns and Statistical Distirbutions* (eds Patil, G.P., Pielou, E.C. & Waters, W.E.). Pennsylvania State University Press, University Park, PA, pp. 99–130.

Brian, M.V. (1953). Species frequencies in random samples from animal populations. *J. Anim. Ecol.*, 22, 57–64.

Brown, J.H., Mehlman, D.H. & Stevens, G.C. (1995). Spatial variation in abundance. *Ecology*, 76, 2028–2043.

Bulmer, M.G. (1974). Fitting poisson lognormal distribution to species-abundance data. *Biometrics*, 30, 101–110.

Burnham, K.P. & Anderson, D.R. (1998). *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. 2nd edn. Springer, New York, NY.

Caswell, H. (1976). Community structure: a neutral model analysis. *Ecol. Monogr.*, 46, 327–354.

Chave, J. (2004). Neutral theory and community ecology. *Ecol. Lett.*, 7, 241–253.

Chiarucci, A., Wilson, J.B., Anderson, B.J. & De Dominicis, V. (1999). Cover versus biomass as an estimate of species abundance: does it make a difference to the conclusions? *J. Veg. Sci.*, 10, 35–42.

Chu, J. & Adami, C. (1999). A simple explanation for taxon abundance patterns. *Int. Natl Acad. Sci.*, 96, 15017–15019.

Clarke, K.R. & Warwick, R.M. (2001). *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation (PRIMER-E)*. Plymouth Marine Laboratory, Plymouth, UK.

Cohen, A.C. (1949). On estimating the mean and standard deviation of truncated normal distributions. *J. Am. Stat. Assoc.*, 44, 518–525.

Cohen, J.E. (1968). Alternate derivations of a species-abundance relation. *Am. Nat.*, 102, 165.

Coleman, B. (1981). Random placement and species area relations. *Math. Biosci.*, 54, 191–215.

Condit, R., Hubbell, S.P., LaFrankie, J.V., Sukumar, R., Manokaran, N., Foster, R.B. *et al.* (1996). Species–area and species–individual relationships for tropical trees: a comparison of three 50-ha plots. *J. Ecol.*, 84, 549–562.

Condit, R., Ashton, P.S., Baker, P., Bunyavejchewin, S., Gunatilleke, S., Gunatilleke, N. *et al.* (2000). Spatial patterns in the distribution of tropical tree species. *Science*, 288, 1414–1418.

Connolly, S.R., Hughes, T.P., Bellwood, D.R. & Karlson, R.H. (2005). Community structure of corals and reef fishes at multiple scales. *Science*, 309, 1363–1365.

Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species–area relationship. *Am. Nat.*, 113, 791–833.

Cotgreave, P. & Harvey, P.H. (1994). Evenness of abundance in bird communities. *J. Anim. Ecol.*, 63, 365–374.

Damuth, J. (1981). Population density and body size in mammals. *Nature*, 290, 699–700.

Damuth, J. (1991). Of size and abundance. *Nature*, 351, 268–269.

Darwin, C. (1859). *On the Origin of Species*. Clows and Sons, London.

Dennis, B. & Patil, G.P. (1984). The gamma distribution and weighted multimodal gamma distributions as models of population abundance. *Math. Biosci.*, 68, 187–212.

Dennis, B. & Patil, G.P. (1988). Applications in ecology. In: *Lognormal Distributions: Theory and Applications* (edsCrow, E.L. & Shimizu, K.). Marcel Dekker, New York, pp. 303–330.

Dewdney, A.K. (1998). A general theory of the sampling process with applications to the 'veil line'. *Theor. Popul. Biol.*, 54, 294–302.

Dewdney, A.K. (2000). A dynamical model of communities and a new species-abundance distribution. *Biol. Bull.*, 198, 152–165.

Diserud, O.H. & Engen, S. (2000). A general and dynamic species abundance model, embracing the lognormal and the gamma models. *Am. Nat.*, 155, 497–511.

Dornelas, M., Connolly, S.R. & Hughes, T.P. (2006). Coral reef diversity refutes the neutral theory of biodiversity. *Nature*, 440, 80–82.

Engen, S. & Lande, R. (1996a). Population dynamic models generating species abundance distributions of the gamma type. *J. Theor. Biol.*, 178, 325–331.

Engen, S. & Lande, R. (1996b). Population dynamic models generating the lognormal species abundance distribution. *Math. Biosci.*, 132, 169–183.

Engen, S., Lande, R., Walla, T. & DeVries, P.J. (2002). Analyzing spatial structure of communities using the two-dimensional poisson lognormal species abundance model. *Am. Nat.*, 160, 60–73.

Enquist, B.J., Sanderson, J. & Weiser, M.D. (2002). Modeling macroscopic patterns in ecology. *Science*, 295, 1835–1837.

Etienne, R.S. (2005). A new sampling formula for neutral biodiversity. *Ecol. Lett.*, 8, 253–260.

Etienne, R.S. (2007). A neutral sampling formula for multiple samples and an 'exact' test of neutrality. *Ecol. Lett.*, 10, 608–618.

Etienne, R.S. & Alonso, D. (2005). A dispersal-limited sampling theory for species and alleles. *Ecol. Lett.*, 8, 1147–1156.

Etienne, R.S. & Olff, H. (2004a). How dispersal limitation shapes species-body size distributions in local communities. *Am. Nat.*, 163, 69–83.

Etienne, R.S. & Olff, H. (2004b). A novel genealogical approach to neutral biodiversity theory. *Ecol. Lett.*, 7, 170–175.

Etienne, R.S. & Olff, H. (2005). Confronting different models of community structure to species-abundance data: a Bayesian model comparison. *Ecol. Lett.*, 8, 493–504.

Etienne, R.S., Alonso, D. & McKane, A.J. (2007a). The zero-sum assumption in neutral biodiversity theory. *J. Theor. Biol.*, http://dx.doi.org/10.1016/j.jtbi.2007.06.010.

Etienne, R.S., Apol, M.E.F., Olff, H. & Weissing, F.J. (2007b). Modes of speciation and the neutral theory of biodiversity. *Oikos*, 116, 241–258.

Evans, M., Hastings, N. & Peacock, B. (1993). *Statistical Distributions*, 2nd edn. John Wiley & Sons, New York.

Fauth, J.E., Bernardo, J., Camara, M., Resetarits, W.J., Jr, Buskirk, J.V. & McCollum, S.A. (1996). Simplifying the jargon of community ecology: a conceptual approach. *Am. Nat.*, 147, 282–286.

Fischer, J. & Lindenmayer, D.B. (2002). Treating the nestedness temperature calculator as a 'black box' can lead to false conclusions. *Oikos*, 99, 193–199.

Fisher, R.A., Corbet, A.S. & Williams, C.B. (1943). The relation between the number of species and the number of individuals in a random sample from an animal population. *J. Anim. Ecol.*, 12, 42–58.

Frontier, S. (1994). Species-diversity as a fractal property of biomass. In: *Fractals in the Natural and Applied Sciences* (ed. Novak, M.) North-Holland Publishing, Amsterdam, pp. 119–127.

Frontier, S. (1985). Diversity and structure in aquatic ecosystems. *Oceanogr. Mar. Biol.*, 23, 253–312.

Galton, F. (1879). The geometric mean in vital and social statistics. *Proc. R Soc. Lond.*, 29, 365–367.

Gaston, K.J. (1996). The multiple forms of the interspecific abundance-distribution relationship. *Oikos*, 76, 211–220.

Gaston, K.J., Blackburn, T.M., Greenwood, J.J.D., Gregory, R.D., Quinn, R.M. & Lawton, J.H. (2000). Abundance-occupancy relationships. *J. Appl. Ecol.*, 37, S39–S59.

Gauch, H.G.J. & Whittaker, R.H. (1972). Coencline simulation. *Ecology*, 53, 446–451.

Gilbert, B., Laurance, W.F., Leigh, E.G., Jr & Nascimento, H.E. (2006). Can neutral theory predict the responses of amazonian tree communities to forest fragmentation? *Am. Nat.*, 168, 304–317.

Gotelli, N.J. & Colwell, R.K. (2001). Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.*, 4, 379–391.

Gray, J.S. (1979). Pollution-induced changes in populations. *Philos. Trans. R Soc. Lond. B*, 286, 545–561.

Gray, J.S. (1987). Species-abundance patterns. In: *Organization of Communities Past and Present* (eds Gee, J.H.R. & Giller, P.S.). Blackwell Science, Oxford, pp. 53–68.

Gray, J.S., Bjorgesaeter, A. & Ugland, K.I. (2005). The impact of rare species on natural assemblages. *J. Anim. Ecol.*, 74, 1131–1139.

Gray, J.S., Bjorgesaeter, A. & Ugland, K.I. (2006). On plotting species abundance distributions. *J. Anim. Ecol.*, 75, 752–756.

Green, J.L. & Plotkin, J.B. (2007). A statistical theory for sampling species abundances. *Ecol. Lett.*, 10, doi:10.1111/j.1461-0248. 2007.01101.x.

Green, J.L., Harte, J. & Ostling, A. (2003). Species richness, endemism and abundance patterns: tests of two fractal models in a serpentine grassland. *Ecol. Lett.*, 6, 919–928.

Gregory, R.D. (2000). Abundance patterns of European breeding birds. *Ecography*, 23, 201–208.

Hamer, K.C., Hill, J.K., Lace, L.A. & Langan, A.M. (1997). Ecological and biogeographical effects of forest disturbance on tropical butterflies of Sumba Indonesia. *J. Biogeogr.*, 24, 67–75.

Hanski, I. (1982). Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos*, 38, 210–221.

Hanski, I. & Gyllenberg, M. (1997). Uniting two general patterns in the distribution of species. *Science*, 275, 397–400.

Harte, J., Kinzig, A.P. & Green, J. (1999). Self-similarity in the distribution and abundance of species. *Science*, 284, 334–336.

Harte, J., Conlisk, E., Ostling, A., Green, J.L. & Smith, A.B. (2005). A theory of spatial structure in ecological communities at multiple spatial scales. *Ecol. Monogr.*, 75, 179–197.

He, F.L. & Legendre, P. (2002). Species diversity patterns derived from species–area models. *Ecology*, 83, 1185–1198.

He, F., Gaston, K.J. & Wu, J. (2002). On species occupancy-abundance models. *Ecoscience*, 9, 119–126.

Heck, K.L.J., Van Belle, G. & Simberloff, D. (1975). Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, 56, 1459–1461.

Hengeveld, R. & Haeck, J. (1981). The distribution of abundance II Models and implications. *Proc. K. Ned. Akad. Wet. C*, 84, 257–284.

Hengeveld, R., Kooijman, S.A.L.M. & Taillie, C. (1979). A spatial model explaining species-abundance curves. In: *Statistical Distributions in Ecological Work* (eds Ord, J.K., Patil, G.P. & Taillie, C.). International Co-operative Publishing House, Fairland, MD, pp. 337–347.

Hill, J.K., Hamer, K.C., Lace, L.A. & Banham, W.M.T. (1995). Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *J. Appl. Ecol.*, 32, 754–760.

Hoagland, B.W. & Collins, S.L. (1997). Gradient models, gradient analysis, and hierarchical structure in plant communities. *Oikos*, 78, 23–30.

Hubbell, S.P. (1979). Tree dispersion, abundance and diversity in a tropical dry forest. *Science*, 203, 1299–1309.

Hubbell, S.P. (2001). *A Unified Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton.

Hubbell, S.P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology*, 87, 1387–1398.

Hughes, R.G. (1986). Theories and models of species abundance. *Am. Nat.*, 128, 879–899.

Hurlbert, S.H. (1971). The nonconcept of species diversity: a critque and alternative parameters. *Ecology*, 52, 577–586.

Hurlbert, A.H. (2004). Species–energy relationships and habitat complexity. *Ecol. Lett.*, 7, 714–720.

Kempton, R.A. & Taylor, L.R. (1974). Log-series and log-normal parameters as diversity discriminants for lepidoptera. *J. Anim. Ecol.*, 43, 381–399.

Kendall, D.G. (1948a). On some modes of population growth leading to Fisher, R.A. logarithmic series distribution. *Biometrika*, 35, 6–15.

Kendall, D.G. (1948b). On the generalized 'birth-and-death' process. *Ann. Math. Stat.*, 19, 1–15.

Labra, F.A., Abades, S. & Marquet, P.A. (2005). Distribution and abundance: scaling patterns in exotic and native bird species. In: *Species Invasions. Insights Into Ecology, Evolution and Biogeography* (eds Sax, D.F., Stachowicz, J.J. & Gaines, S.D.). Sinauer Associates, Sunderland, MA, pp. 421–446.

Lakatos, I. (1978). Introduction: science and pseudoscience. In: *The Methodology of Scientific Research Programs* (eds Worrall, J. & Currie, G.). Cambridge University Press, Cambridge, pp. 1–8.

Lambshead, P.J.D., Platt, H.M. & Shaw, K.M. (1983). The detection of differences among assemblages of marine benthic species based on an assessment of dominance and diversity. *J. Nat. His.*, 17, 859–874.

Latimer, A.M., Silander, J.A. & Cowling, R.M. (2005). Neutral ecological theory reveals isolation and rapid speciation in a biodiversity hot spot. *Science*, 309, 1722–1725.

Lawton, J.H. (1993). Range, population abundance and conservation. *Trends Ecol. Evol.*, 8, 409–413.

Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology*, 73, 1943–1967.

Lewontin, R.C., Ginzburg, L.R. & Tuljapurkar, S.D. (1978). Heterosis as an explanation for large amounts of genic polymorphism. *Genetics*, 88, 149–170.

Mac Nally, R. (2007). Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. *Am. Nat.*, in press.

MacArthur, R. (1957). On the relative abundance of bird species. *Proc. Natl Acad. Sci.*, 43, 293–295.

MacArthur, R. (1960). On the relative abundance of species. *Am. Nat.*, 94, 25–36.

MacArthur, R. (1966). Note on Mrs Pielou's comments. *Ecology*, 47, 1074.

MacLachlan, G. & Peel, D. (2000). *Finite Mixture Models*. John Wiley & Sons, New York.

Magurran, A.E. (2004). *Measuring Biological Diversity*, 2nd edn. Blackwell, Oxford.

Magurran, A.E. (2005). Species abundance distributions: pattern or process? *Funct. Ecol.*, 19, 177–181.

Magurran, A.E. (2007). Species abundance distributions over time. *Ecol. Lett.*, 10, 347–354.

Magurran, A.E. & Henderson, P.A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature*, 422, 714–716.

Mandelbrot, B. (1965). Information theory and psycholinguistics. In: *Scientific Psychology: Principles and Applications*, (ednWolman, B.A. & Nagel, E.N.). Basic Books, New York, pp. 350–368.

Marks, C.O. & Lechowicz, M.J. (2006). Alternative designs and the evolution of functional diversity. *Am. Nat.*, 167, 55–66.

Marquet, P.A., Navarrete, S.A. & Castilla, J.C. (1990). Scaling population density to body size in rocky intertidal communities. *Science*, 250, 1125–1127.

Marquet, P.A., Keymer, J.A. & Cofre, H. (2003). Breaking the stick in space: of niche models, metacommunities and patterns in the relative abundance of species. In: *Macroecology: Concepts and Consequences* (eds Blackburn, T.M. & Gaston, K.J.). Blackwell Science, Oxford, pp. 64–86.

Marquet, P.A., Fernández, M., Navarrete, S.A. & Valdivinos, C. (2004). Diversity emerging: towards a deconstruction of biodiversity patterns. In: *Frontiers of Biogeography: New Directions in the Geography of Nature* (ed Heaney, M.L.a.L.R.). Cambridge University Press, Cambridge, pp. 192–209.

Martinez, W.L. & Martinez, A.R. (2002). *Computational Statistics Handbook With MATLAB*. Chapman & Hall/CRC, Boca Raton.

Maurer, B.A. (1990). The relationship between distribution and abundance in a patchy environment. *Oikos*, 58, 181–189.

May, R.M. (1975). Patterns of species abundance and diversity. In: *Ecology and Evolution of Communities* (eds Cody, M.L. & Diamond, J.M.). Belknap Press of Harvard University Press, Cambridge MA, pp. 81–120.

McAlister, D. (1879). The law of the geometric mean. *Proc. R Soc. Lond.*, 29, 367–376.

McGill, B. (2003a). Strong and weak tests of macroecological theory. *Oikos*, 102, 679–685.

McGill, B.J. (2003b). Does Mother Nature really prefer rare species or are log-left-skewed SADs a sampling artefact? *Ecol. Lett.*, 6, 766–773.

McGill, B.J. (2003c). A test of the unified neutral theory of biodiversity. *Nature*, 422, 881–885.

McGill, B.J. (2006). A renaissance in the study of abundance. *Science*, 314, 770–771.

McGill, B. & Collins, C. (2003). A unified theory for macroecology based on spatial patterns of abundance. *Evol. Ecol. Res.*, 5, 469–492.

McGill, B.J., Hadly, E.A. & Maurer, B.A. (2005). Community inertia of Quaternary small mammal assemblages in North America. *Proc. Natl Acad. Sci.*, 102, 16701–16706.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006a). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

McGill, B.J., Maurer, B.A. & Weiser, M.D. (2006b). Empirical evaluation of the neutral theory. *Ecology*, 87, 1411–1423.

Motomura, I. (1932). On the statistical treatment of communities. *Zool. Mag.*, 44, 379–383.

Mouillot, D. & Lepretre, A. (2000). Introduction of relative abundance distribution (RAD) indices, estimated from the rank-frequency diagrams (RFD), to assess changes in community diversity. *Environ. Monit. Assess.*, 63, 279–295.

Mouillot, D., Lepretre, A., Andrei-Ruiz, M.C. & Viale, D. (2000). The Fractal model: a new model to describe the species accumulation process and relative abundance distribution (RAD). *Oikos*, 90, 333–342.

Munoz, F., Couteron, P., Ramesh, B. & Etienne, R. (2007). Estimating parameters of neutral communities: from one single large to several small samples. *Ecology*, (in press).

Murray, B.R. & Westoby, M. (2000). Properties of species in the tail of rank-abundance curves: the potential for increase in abundance. *Evol. Ecol. Res.*, 2, 583–592.

Murray, B.R., Rice, B.L., Keith, D.A., Myerscough, P.J., Howell, J., Floyd, A.G. *et al.* (1999). Species in the tail of rank-abundance curves. *Ecology*, 80, 1806–1816.

Murray, B.R., Thrall, P.H., Gill, A.M. & Nicotra, A.B. (2002). How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Aust. Ecol.*, 27, 291–310.

Nee, S. (2003). The unified phenomenological theory of biodiversity. In: *Macroecology: Concepts and Consequences* (eds Blackburn, T.M. & Gaston, K.J.). Blackwell Science, Oxford, pp. 31–44.

Nee, S., Harvey, P.H. & May, R.M. (1991). Lifting the veil on abundance patterns. *Proc. R Soc Lond Ser. B Biol. Sci.*, 243, 161–163.

Nekola, J.C. & Brown, J.H. (2007). The wealth of species: ecological communities, complex systems and the legacy of Frank Preston. *Ecol. Lett.*, 10, 188–196.

Ockham, W.. (1495). *Quaestiones et decisiones in quattuor libros Sententiarum Petri Lombardi* Editioni Lugdenensi, i, dist. 27, qu. 2, K.

Olszewski, T.D. (2004). A unified mathematical framework for the measurement of richness and evenness within and among multiple communities. *Oikos*, 104, 377–387.

Patil, G.P. & Taillie, C. (1982). Diversity as a concept and its measurement. *J. Am. Stat. Assoc.*, 77, 548–561.

Peters, R.H. (1991). *A Critique for Ecology*. Cambridge University Press, Cambridge.

Pielou, E.C. (1975). *Ecological Diversity*. John Wiley & Sons, New York.

Pielou, E.C. (1977). *Mathematical Ecology*. John Wiley & Sons, New York.

Platt, J.R. (1964). Strong inference. *Science*, 146, 347–353.

Plotkin, J.B. & Muller-Landau, H.C. (2002). Sampling the species composition of a landscape. *Ecology*, 83, 3344–3356.

Preston, F.W. (1948). The commonness and rarity of species. *Ecology*, 29, 254–283.

Preston, F.W. (1960). Time and space and the variation of species. *Ecology*, 41, 611–627.

Pueyo, S. (2006). Diversity: between neutrality and structure. *Oikos*, 112, 392–405.

Raunkiaer, C. (1909). Formationsundersogelse og Formationsstatistik. *Bot. Tidskr.*, 30, 20–132.

Ricklefs, R.E. (2003). A comment on Hubbell's zero-sum ecological drift model. *Oikos*, 100, 185–192.

Riitters, K.H., O'Neill, R.V., Hunsaker, C.T., Wickham, J.D., Yankee, D.H., Timmins, S.P. *et al.* (1995). A factor analysis of landscape pattern and structure metrics. *Landsc. Ecol.*, 10, 23–39.

Robbins, C.S., Bystrak, D. & Geissler, P.H. (1986). *The Breeding Bird Survey: Its First Fifteen Years, 1965–1979*. US Department of the Interior Fish and Wildlife Service, Washington, DC.

Rosenzweig, M.L. (1995). *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.

Rosenzweig, M.L. & Abramsky, Z. (1997). Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. *Evol. Ecol.*, 11, 733–756.

Rosenzweig, M.L. & Lomolino, M.V. (1997). Who gets the short bits of the broken stick. In: *The Biology of Rarity: Causes and Consequences of Rare-Common Differences* (eds Kunin, W.E. & Gaston, K.J.). Chapman & Hall, London, pp. 63–90.

Rosindell, J. & Cornell, S.J. (2007). Species-area relationships from a spatially explicit neutral model in an infinite landscape. *Ecol. Lett.*, 7, 586–595.

Russo, S.E., Robinson, S.K. & Terborgh, J. (2003). Size-abundance relationships in an amazonian bird community: implications for the energetic equivalence rule. *Am. Nat*, 161, 267–283.

Sanders, H.L. (1968). Marine benthic diversity: a comparative study. *Am. Nat.*, 102, 243–282.

Savage, V.M., Gillooly, J.F., Brown, J.H., West, G.B. & Charnov, E.L. (2004). Effects of body size and temperature on population growth. *Am. Nat.*, 163, 429–441.

Shipley, B., Vile, D. & Garnier, E. (2006). From plant traits to plant communities: a statistical mechanistic approach to biodiversity. *Science*, 314, 812–814.

Simberloff, D.S. (1972). Properties of the rarefaction diversity measurement. *Am. Nat.*, 106, 414–418.

Simon, H.A. (1955). On a class of skew distribution functions. *Biometrika*, 42, 425–440.

Soule, M.E. (1986). *Conservation Biology: The Science of Scarcity and Diversity*. Sinauer Associates, Sunderland, MA.

Southwood, T.R.E. (1996). The Croonian lecture, 1995: natural communities: structure and dynamics. *Philos. Trans. Biol. Sci.*, 351, 1113–1129.

Stirling, G. & Wilsey, B. (2001). Empirical relationships between species richness, evenness, and proportional diversity. *Am. Nat.*, 158, 286–299.

Sugihara, G. (1980). Minimal community structure: an explanation of species-abundance patterns. *Am. Nat.*, 116, 770–787.

Sugihara, G., Bersier, L.F., Southwood, T.R.E., Pimm, S.L. & May, R.M. (2003). Predicted correspondence between species abundances and dendrograms of niche similarities. *Proc. Natl Acad. Sci. USA.*, 100, 5246–5251.

Thibault, K.M., White, E.P. & Ernest, S.K.M. (2004). Temporal dynamics in the structure and composition of a desert rodent community. *Ecology*, 85, 2649–2655.

Tokeshi, M. (1993). Species abundance patterns and community structure. *Adv. Ecol. Res.*, 24, 111–186.

Tokeshi, M. (1996). Power fraction: a new explanation of relative abundance patterns in species-rich assemblages. *Oikos*, 75, 543–550.

Tuljapurkar, S.D. (1990). *Population Dynamics in Variable Environments*. Springer-Verlag, New York.

Ugland, K.I. & Gray, J.S. (1982). Lognormal distributions and the concept of community equilibrium. *Oikos*, 39, 171–178.

Ugland, K.I. & Gray, J.S. (1983). Reanalysis of Caswell's neutral models. *Ecology*, 64, 603–605.

Ugland, K.I., Gray, J.S. & Ellingsen, K.E. (2003). The species-accumulation curve and estimation of species richness. *J. Anim. Ecol.*, 72, 888–897.

Ugland, K.I., Lambshead, P.J.D., McGill, B., Gray, J.S., O'Dea, N., Ladle, R.J. *et al.* (2007). Modelling dimensionality in species abundance distributions: description and evaluation of the Gambin model. *Evol. Ecol. Res.*, 9, 1–12.

Ulrich, W. & Ollik, M. (2004). Frequent and occasional species and the shape of relative-abundance distributions. *Divers. Distrib.*, 10, 263–269.

Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. (2003). Neutral theory and relative species abundance in ecology. *Nature*, 424, 1035–1037.

Warwick, R.M. (1986). A new method for detecting pollution effects on marine macrobenthic communities. *Mar. Biol.*, 92, 557–562.

Watterson, G.A. (1974). The sampling theory of selectively neutral alleles. *Adv. Appl. Probability*, 6, 463–488.

Webb, C.O., Ackerly, D.D., McPeek, M.A. & Donoghue, M.J. (2002). Phylogenies and community ecology. *Annu. Rev. Ecol. Syst.*, 33, 475–505.

Weiher, E. & Keddy, P.A. (1999). Relative abundance and evenness patterns along diversity and biomass gradients. *Oikos*, 87, 355.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J. & Enquist, B.J. (2007). Relationships between body size and abundance in ecology. *Trends Ecol. Evol.*, 22, 323–330.

Whittaker, R.H. (1960). Vegetation of the Siskiyou mountains, Oregon and California. *Ecol. Monogr.*, 30, 279–338.

Whittaker, R.H. (1965). Dominance and diversity in land plant communities. *Science*, 147, 250–260.

Whittaker, R.H. (1967). Gradient analysis of vegetation. *Biol. Rev.*, 42, 207–264.

Whittaker, R.H. (1975). *Communities and Ecosystems*, 2nd edn. MacMillan Publishers, New York.

Wiens, J.A. (1989). Spatial scaling in ecology. *Funct. Ecol.*, 3, 385–397.

Williams, C.B. (1964). *Patterns in the Balance of Nature*. Academic Press, London.

Williamson, M. & Gaston, K.J. (2005). The lognormal distribution is not an appropriate null hypothesis for the species abundance distribution. *J. Anim. Ecol.*, 74, 1–14.

Wilsey, B.J., Chalcraft, D.R., Bowles, C.M. & Willig, M.R. (2005). Relationships among indices suggest that richness is an incomplete surrogate for grassland biodiversity. *Ecology*, 86, 1178–1184.

Wilson, J.B. (1991). Methods for fitting dominance diversity curves. *J. Veg. Sci.*, 2, 35–46.

Wilson, J.B. (1993). Would we recognise a broken-stick community if we found one? *Oikos*, 67, 181–183.

Wilson, J.B., Wells, T.C.E., Trueman, I.C., Jones, G., Atkinson, M.D., Crawley, M.J. *et al.* (1996). Are there assembly rules for plant species abundance? An investigation in relation to soil resources and successional trends? *J. Ecol.*, 84, 527–538.

Wilson, J.B., Gitay, H., Steel, J.B. & King, W.M. (1998). Relative abundance distributions in plant communities: effects of species richness and of spatial scale. *J. Veg. Sci.*, 9, 213–220.

Wilson, W.G., Lundberg, P., Vazquez, D.P., Shurin, J.B., Smith, M.D., Langford, W. *et al.* (2003). Biodiversity and species interactions: extending Lotka-Volterra community theory. *Ecol. Lett.*, 6, 944–952.

Winemiller, K.O. (1990). Spatial and temporal variation in tropical fish trophic networks. *Ecol. Monogr.*, 60, 331–367.

Wootton, J.T. (2005). Field parameterization and experimental test of the neutral theory of biodiversity. *Nature*, 433, 309–312.

Wright, D.H., Patterson, B.D., Mikkelson, G.M., Cutler, A. & Atmar, W. (1998). A comparative analysis of nested subset patterns of species composition. *Oecologia*, 113, 1–20.

Yin, Z.Y., Ren, H., Zhang, Q.M., Peng, S.L., Guo, Q.F. & Zhou, G.Y. (2005). Species abundance in a forest community in south China: a case of poisson lognormal distribution. *J. Integr. Plant Biol.*, 47, 801–810.

Yule, G.U. (1924). A mathematical theory of evolution based on the conclusions of Dr J C Willis. *Philosophical Transactions of the Royal Society B*, 213, 21–87.

Zipf, G.K. (1949). *Human Behaviour and the Principle of Least-Effort*. Addison-Wesley Publishing Co., Cambridge, MA.