

REVIEW

On the species abundance distribution in applied ecology and biodiversity management

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Summary

1. The species abundance distribution (SAD) is an important concept in ecology, and much work has focused on the SAD in a theoretical context. However, less focus has been placed on the utility of SADs in applied ecology and biodiversity management, which therefore forms the focus of the present article. We illustrate that study of the SAD allows inferences beyond those that flow from many simple diversity indices, enabling workers to identify patterns in the commonness and rarity of species in a community.

2. First, we discuss how incorporating SAD analyses into the study of ecological communities can generate useful information for the management of biodiversity. In particular, we argue that deconstructing ecological assemblages into various subsets and analysing how each subset contributes to the overall SAD can reveal patterns of interest to managers. Secondly, we review the many applications of SADs in applied ecological fields, including disturbance ecology, conservation planning and conservation biological control.

3. Using examples we show that the SAD can be useful in applied ecology as it is visually intuitive, easy to implement in a broad variety of ecological contexts, and does not require substantial species-specific data. We provide a summary of the various methods available for plotting the SAD and illustrate how each method provides information of value for applied ecologists.

4. Using empirical and simulated data, we show that the SAD can provide early warning of the effects of disturbance on ecological communities and that a number of SAD models represent useful tools for comparing communities in a management context.

5. *Synthesis and applications.* Applied ecologists require tools that allow for relatively quick assessments of ecosystem health and/or the success of management prescriptions aimed at ameliorating the effects of disturbance. We demonstrate that the methods reviewed herein provide such tools and that the species abundance distribution (SAD) has additional applied uses beyond traditional applications in disturbance ecology. We hope that this synthesis will provide a catalyst for advancing a more utilitarian SAD research agenda.

Key-words: community structure, conservation biogeography, disturbance ecology, macroecology, multimodal species abundance distribution, scaling, species abundance distribution

Introduction

The species abundance distribution (SAD) characterizes the distribution of abundances of all species within a

sample or ecological community. The observation that most species are relatively rare with only a few being common is often described as one of the few ecological laws (McGill *et al.* 2007). The SAD is an important concept in ecology and macroecology, being interesting in its own right as well as providing the theoretical foundation for exploration of other ecological patterns, such as the

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distance–decay relationship and the species–area relationship (SAR; Preston 1948; McGill *et al.* 2007; Whittaker & Fernández-Palacios 2007). Around 30 different SAD models have been proposed, with the most commonly used being the log-normal (Preston 1948) and the logseries (Fisher, Corbet & Williams 1943). While SADs have been researched for over seventy years (e.g. Fisher, Corbet & Williams 1943), there has been a resurgence of interest over the last decade (e.g. McGill *et al.* 2007). However, much of this recent work has been on theoretical aspects of the pattern, and less focus has been placed on the utility of SADs as a tool to provide useful information in applied ecology, conservation and management. For instance, a number of general SAD reviews have been published (e.g. May 1975; Magurran 2004; McGill *et al.* 2007; McGill 2011), but few discuss the applied uses of SADs (for an exception, see Dornelas, Soykan & Ugland 2011). Global environmental change and disturbance to biotic communities resulting from habitat loss, pollution and invasive species, amongst other drivers, represent substantial pressures on biodiversity (Sala *et al.* 2000), in the light of which applied ecologists and biodiversity managers require accurate, easy to use and intuitive methods for measuring the impacts of the aforementioned drivers of biodiversity decline (Mouillot *et al.* 2013). It is also necessary that these methods allow workers to compare communities which differ in species richness, an issue which plagues many traditional diversity metrics. We believe the SAD represents such a toolkit. Thus, the distinctive purpose of this review is to synthesize the information and recent advances relating to the use of the SAD in applied ecology. To achieve this aim, we have split the review into two broad sections regarding the utility of SADs in applied ecology: (1) a discussion on how incorporating the SAD into the study of ecological communities can generate useful information for the management of biodiversity and (2) a review of the application, and potential application, of SADs in biodiversity conservation and management. In the first section, we review the recent literature on combining SADs with an assemblage deconstruction approach in order to illustrate how the analysis of complete assemblages (i.e. all sampled species) can obscure important abundance patterns in species of conservation and management concern. We use recent case studies of multimodal SADs to highlight the types of beneficial information that can be derived from this approach. The second section focuses more on the actual usage of SADs in conservation, including application of SADs in measuring ecosystem health, and for conservation planning frameworks.

ON PLOTTING SPECIES ABUNDANCE DISTRIBUTIONS

Before progressing, it is necessary to review briefly the two main methods for plotting SADs, as both are

discussed throughout the paper. First, **the SAD can be visualized as a histogram of the number of individuals on the x-axis and the number of species represented by a particular abundance on the y-axis.** The numbers of individuals are generally binned into octaves using a variety of different methods (see Gray, Bjørgesæter & Ugland 2006; Matthews & Whittaker 2014). The use of binning in SAD studies has been criticized as it results in the loss of information (Gray, Bjørgesæter & Ugland 2006). Thus, **a number of studies use a different plotting method, termed rank abundance plots (e.g. Foster & Dunstan 2010; see Matthews & Whittaker 2014). Rank abundance plots/diagrams (RADs) are plots of abundance (untransformed or log-transformed) against rank order, where rank one corresponds to the species with the highest abundance and so on.** Generally, species with the same abundance are assigned increasing ranks; for example, three species in a sample represented by five individuals might be given the ranks of 10, 11 and 12. However, it may in fact be preferable to assign such species the same rank, in this case 10, 10 and 10. RADs are useful in that they can sometimes reveal differences in model fits not apparent when using histograms (Fattorini 2005). Fattorini (2005) has recently shown that the geometric series and broken stick SAD models (see Matthews & Whittaker 2014) can be fitted using linear regression and RAD plots. His analyses demonstrate that when the abundance data are log-transformed, a linear relationship indicates that the SAD follows a geometric series, while the broken stick model is supported in cases where a linear relationship emerges following log-transformation of the rank axis.

Section 1: Using the species abundance distribution to derive information on ecological community characteristics for applied purposes

The efficient management of ecological communities (generally a unit of management interest, e.g. typical UK nature reserves) is reliant on detailed and accurate information regarding particular community characteristics, for example the abundance of species of conservation interest (Newman 1993). Typically, such information is presented in the form of simple counts of the number of species, or occasionally a simple diversity index is calculated, such as the Shannon–Wiener index. However, this type of information can only reveal so much, and we would argue that looking at the full abundance spectrum is a much more elucidative approach (below, Dornelas *et al.* 2009; Dornelas, Soykan & Ugland 2011; Sæther, Engen & Grøtan 2013). We focus this section of the review on a recent area of research interest which we feel has particular potential for applied ecology, but which has not been discussed in recent SAD reviews: combining SADs with an assemblage deconstruction approach.

THE ASSEMBLAGE DECONSTRUCTION APPROACH

Typically, empirical ecological and macroecological analyses are based on lists of all species encountered during a sampling exercise, for example all birds seen or heard in a patch of forest. However, it has become increasingly apparent that the aggregation in a sample of species with differences in key ecological properties, such as body size, dispersal ability or habitat affinity and specialization, can act to obscure patterns of interest for particular subsets of species, a theory we have termed the amalgamation hypothesis in previous work (Matthews, Borges & Whittaker 2014). Thus, a number of recent studies have focused on splitting samples into various subsets prior to analysis and then exploring patterns of interest in each subset separately (e.g. Magurran & Henderson 2003; Ulrich & Zalewski 2006; Bommarco *et al.* 2010). For example, in a recent paper, we have shown that the amalgamation of specialist and generalist bird species in forest fragment data sets can act to mask the loss of specialist species, generally those species of most conservation concern, in response to habitat insularization (i.e. generalists depress the slope of the island SAR; Matthews, Cottee-Jones & Whittaker 2014; see also Bommarco *et al.* 2010). To take another example, this time in the context of SADs, Labra, Abades & Marquet (2005) used a deconstruction approach to look at invasive and native species and found that for US birds, on average, invasive species obtain higher maximum abundances than native species.

This, it is argued, is due to the higher habitat generalization of many invasive species, which allows them to reach higher abundances within a given community (Labra, Abades & Marquet 2005). Failure to take into account the effect on analyses of the amalgamation of different types of species in samples, for instance in the above cases generalist and invasive species, may result in inappropriate conservation plans being formulated (Matthews, Cottee-Jones & Whittaker 2014). A deconstruction approach for macroecology in general is advocated and described in depth by Marquet *et al.* (2004).

ANALYSIS OF MULTIMODAL SPECIES ABUNDANCE DISTRIBUTIONS WITHIN A DECONSTRUCTION FRAMEWORK

While the possibility has long been recognized, it has become increasingly apparent that many SADs may in fact be multimodal, that is characterized by multiple distinct modes (e.g. Pielou 1969; Dornelas & Connolly 2008; Vergnon, van Nes & Scheffer 2012; Matthews, Borges & Whittaker 2014). A number of explanations have been put forward to explain multimodal SADs, including emergent neutrality theory (Vergnon, van Nes & Scheffer 2012; but see Barabás *et al.* 2013) and the possibility that they simply represent statistical artefacts (Gaston 1994; McGill *et al.* 2007). A more detailed history of multimodal SAD research is presented in Table 1. However,

Table 1. The history of multimodal species abundance distribution research

Study	Main finding
Pielou (1969); Šizling <i>et al.</i> (2009)	One of the first studies to recognize the possibility of multimodal SADs, stating that increasing a sample to include a broader range of taxa (e.g. expanding from a focus on warblers to all birds), might result in the combination of several logseries distributions, each with its own set of parameters. More recently, Šizling <i>et al.</i> (2009) have discussed how incorporating multiple areas and a variety of taxa within a sample can result in a SAD that is a proportional sum of different partial SADs
Ugland & Gray (1982)	A problem with using the log-normal distribution to model SADs is that it assumes equal density probabilities across the species (symmetry), but in reality, there is a general pattern of asymmetry as communities are comprised of three distinct abundance groups, roughly translated as rare, intermediately abundant and common. Within each group, the SAD is symmetric, which leads to a mixture of three log-normal distributions when focusing on the whole assemblage
Gray, Bjørgesæter & Ugland (2005)	Found strong evidence of bimodal log-normal distributions for a mixture of marine and terrestrial data sets.
Dornelas & Connolly (2008)	Fitted a combination of one- to four-mode Poisson log-normal (PLN) distributions, in addition to the logseries, for a large sample of coral communities, Australia, and compared the various distributions using maximum-likelihood methods. At the scale of the entire sample, the three-mode PLN had the greatest support, but as the four-mode model was within an AIC of 2 of the three-mode model, this can also be concluded to have strong support
Borges <i>et al.</i> (2008)	The SADs of arthropod communities on Terceira Island, Azores, could be deconstructed into three distinct abundance groups (abundant, intermediate and rare)
Dornelas <i>et al.</i> (2009)	Found that environmental heterogeneity underpinned multimodal SADs of weed seed bank communities
Vergnon, van Nes & Scheffer (2012)	Tested a number of data sets representing various taxa and found strong evidence of multimodality. This indicates that multimodality may be more common than previously thought: it has simply been overlooked
Matthews, Borges & Whittaker (2014)	Using the methodology of Dornelas & Connolly (2008), it was found that a two-mode PLN provided a better fit than the unimodal PLN and logseries for a number of Azorean arthropod assemblages at a variety of spatial scales

perhaps the most widely accepted explanation is the aforementioned amalgamation hypothesis (e.g. Alonso, Ostling & Etienne 2008). In this regard, analysis of multimodal SADs often reveals interesting information relating to community structure because the different modes in the distribution have often been found to represent clusters of different types of species (Ugland & Gray 1982; Borges *et al.* 2008; Matthews, Borges & Whittaker 2014). That is, species are more similar, according to some trait, to others within clusters than between clusters. For instance, one assemblage division which has proved enlightening in SAD studies has been into core and satellite species subsets. Conceptually, core species represent the constituent members of any ecological community and are predicted to be structured according to traditional niche-based mechanisms (Ulrich & Zalewski 2006). Satellite species are those species only occasionally found in any community (i.e. mostly immigrants from outside the local species pool) and are predicted to be governed by stochastic processes, largely random dispersal. Using a core–satellite division, Magurran & Henderson (2003), who focused on an estuarine fish community in the UK over a period of 21 sampling years, discovered that those species which are relatively abundant throughout the record and possess specialized estuarine habitat requirements (the ‘core’ species) are characterized by a log-normal distribution. In contrast, the species with low abundances, infrequent records in the data set and different habitat requirements (the ‘satellite’ species) follow simple Poisson processes and are characterized by a logseries distribution (Magurran & Henderson 2003). The two different sets of species leave different signals within the SAD and when combined result in a distribution with more rare species than predicted by the standard log-normal model (for further examples, see Gray, Bjørgesæter & Ugland 2005; Ulrich & Zalewski 2006; Unterseher *et al.* 2011). It is important to remember, however, that any division of an assemblage into core and satellite species is a simplification of reality. Empirical assemblages represent a continuum of species types, and workers must be careful not to introduce artefacts into analyses when splitting species into binary categories.

More recently, Matthews, Borges & Whittaker (2014) used a null model approach to show that the SADs of Azorean forest arthropods were frequently significantly bimodal, with the rarer mode of species predominantly comprising satellite species and the common mode largely comprising core species. Many of the satellite species in the rarer modes were as follows: (a) species introduced to the Azores and (b) also classified as tourist species (*sensu* Borges *et al.* 2008). Tourist species were defined as species present in higher abundances in more anthropogenic land use types surrounding the native forest patches (e.g. agricultural pastures or exotic forest plantations) and for which it was assumed that native forest was not primary habitat (Matthews, Borges & Whittaker 2014). Thus, although occurring rarely in the samples, they were not

species of conservation concern. The core–satellite dichotomy used in conjunction with a multimodal SAD model in the above study was useful as it allowed focus on the abundance of the different types of species and showed that a significant proportion of the ‘rare’ species in the forest were in fact species which managers would not want to conserve (e.g. introduced species; see also Matthews, Cottee-Jones & Whittaker 2014). Dornelas *et al.* (2009) have also shown that fitting multimodal SAD models to weed communities in agroecosystems can generate useful information about how weed species respond to environmental heterogeneity (discussed below).

In sum, it has become increasingly apparent that the amalgamation of multiple groups of species within a sample can mask patterns that may be of considerable interest to managers. A natural next step then is to deconstruct full assemblages/samples into different subsets and to explore patterns in the subsets separately. This does not have to add too much complexity to data collection and analysis; simple divisions (e.g. core and satellite species, specialist and generalists) can be informative.

Section 2: The species abundance distribution in biodiversity management and conservation

Although not as widespread in the management and conservation literature as other macroecological patterns (e.g. the SAR), SADs are a potentially useful tool for conservation scientists and managers as they can be used to ‘define’ rarity in a particular community. Conservation practices generally focus on rare species within a delineated protected area boundary (Gaston 1994), and a SAD can provide evidence of the level of rarity of particular species of interest relative to other species (McGill 2011) and thus extinction risk and associated conservation action. In addition, changes in the empirical SAD can act as an early warning for the effects of disturbance on biodiversity, as the shape of the SAD can change markedly before any local extinctions occur (Hågvar 1994; Mouillot *et al.* 2013). Disturbance to ecological communities arising from drivers such as habitat loss, invasive species and pollution is a pervasive feature of modern times (Sala *et al.* 2000), and there is thus an exigent need for the development of tools that allow for relatively quick assessments of ecosystem health and/or the success of management prescriptions aimed at ameliorating the effects of disturbance (Mouillot *et al.* 2013). We argue here that the SAD represents an example of such a tool, and we use this section to review a number of particularly promising areas of application.

DISTURBANCE AND ECOSYSTEM HEALTH

An area of biodiversity conservation and management in which it has long been argued that SADs represent a potentially useful tool is in acting as an ecological indicator to determine the effects of pollution, and disturbance

more generally, on biotic communities (Gray *et al.* 1979; Tokeshi 1993; Dornelas, Soykan & Ugland 2011). Disturbance plays a central role in structuring communities, and the prevalence of human-induced disturbance has resulted in wide-ranging effects on biodiversity and ecosystem functioning and, in particular, species abundances. Characterizing community structure and comparing structure across communities are problematic as ecological communities are complex and contain a large amount of information. Several nonparametric indices (e.g. the Simpson Diversity Index) have been developed to condense this information and allow easier comparison between communities. However, such indices can oversimplify the complex structural nature of communities and most are not independent of sampling intensity (Mouillot & Lepretre 2000; Dornelas, Soykan & Ugland 2011). Thus, it has been argued that the full SAD should be used to compare communities (e.g. Mouillot & Lepretre 2000; Kim, Cho & Chon 2013; Sæther, Engen & Grøtan 2013). Furthermore, ecological disturbance can have varying impacts on different parts of the SAD (e.g. common or rare species), a fact which is obscured when focusing on individual diversity indices. Kúrka, Šizling & Rosindell (2010) have also argued that the SAD can be used to identify the impacts of disturbance in a delineated area. These authors show that disturbance affects the spatial distribution of individuals in an assemblage and thus that disturbance alters the shape of the SAD through affecting either or both of (a) the degree of spatial autocorrelation in the area and (b) the degree of turnover between subplots within the area.

The log-normal distribution has been proposed as a means of accurately modelling undisturbed communities and thus represents a measure by which deviation from such 'equilibrium' can be measured (e.g. May 1975; Hill *et al.* 1995). The suitability of the log-normal as a general SAD model derives from the central limit theorem, in which a large number of biotic and abiotic factors affecting population sizes act multiplicatively to generate a log-normal distribution of abundances (May 1975). In contrast, SADs in disturbed communities have been shown to follow distributions close to the logseries (e.g. Hill *et al.* 1995). Early papers on the topic (e.g. Gray & Mirza 1979; Gray *et al.* 1979) focused on the effects of organic pollution on marine benthic communities, largely in Norway and Scotland, and used departure from log-normality to indicate the impact of pollution on community structure (but see Tokeshi 1993 for criticisms of their method). Following a mild pollution event, departure from log-normality was argued to result as a few species became more abundant, while most species became rarer or became extirpated from the system. Recent papers have provided further evidence of the utility of this approach (e.g. Tang *et al.* 2010; Kim, Cho & Chon 2013). For example, Kim, Cho & Chon (2013) found that the SAD of macroinvertebrates in non-polluted streams (a key target group for ecosystem health) in Korea was best fitted by a log-normal model, while the SAD of macroinvertebrates in pol-

luted streams was better fitted by a geometric model (a model with a similar curve shape to the logseries, in which the abundance of a particular species is proportional to the amount of limiting resource they have apportioned).

This transition from log-normal to logseries shaped curves is illustrated in Fig. 1. Here, we have simulated an undisturbed community by generating random data to follow a log-normal distribution (Fig. 1a). We then modelled a natural perturbation to the system by randomly sampling 5% of the individuals (i.e. removing 95% of the individuals) (Fig. 1b). Ecologically, this simulated perturbation represents a situation in which populations of rare species are most likely to go locally extinct. This simulation is also similar to the approach adopted by Green & Plotkin (2007), in which individuals were sampled in a spatially explicit manner from regional SADs to examine the scaling relationships between sample and regional-scale SADs. Plotting the SAD of the undisturbed and disturbed community (i.e. before and after) reveals the shift from a log-normal to a logseries distribution (Fig. 1). Comparing the fit of the Poisson log-normal (here we have used the zero-truncated form) and logseries distributions provides a more rigorous means of determining deviation from the log-normal, and using Akaike's information criterion (AIC) to compare the two models reveals that in Fig. 1a the zero-truncated log-normal provides a superior fit, while in Fig. 1b, the logseries is the better-fitting model (AIC values are given in Fig. 1).

It is important to note that the use of the log-normal in such circumstances is based on the assumption that it provides a good fit to the undisturbed data, but other distributions, including the logseries, have often been found to fit data from undisturbed systems better (e.g. Syrek *et al.* 2006), while disturbed communities have been shown to follow a log-normal distribution with similar parameters to undisturbed communities (Nummelin 1998). Furthermore, under acute stress, communities have been observed to go from logseries back to log-normal, but with very different parameters (Hågvar 1994). Due to these issues, other SAD models have been proposed as more accurate descriptors of undisturbed and disturbed communities, for example the Zipf-Mandelbrot model (Mouillot & Lepretre 2000), geometric series (Kim, Cho & Chon 2013), broken stick and negative binomial distribution models (Syrek *et al.* 2006), and power law and niche partitioning models (Tang *et al.* 2010). Thus, fitting a suite of models to both undisturbed and disturbed communities can be informative (e.g. Syrek *et al.* 2006). Additionally, instead of attempting to detect deviation from log-normal to logseries distributions, the aforementioned multimodal SAD models can be used to measure the impact of disturbance. For example, Dornelas *et al.* (2009) showed that for agricultural weed communities, homogenous environments were characterized by a standard unimodal log-normal SAD. However, weed communities in increasingly heterogeneous environments (e.g. due to tillage and nitrogen

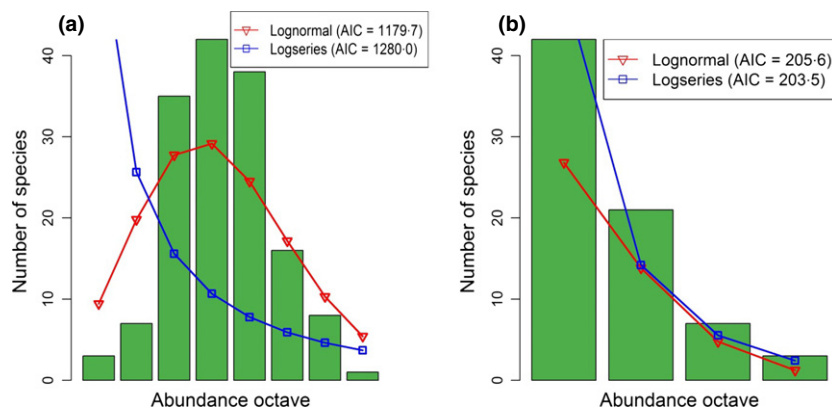


Fig. 1. Using the species abundance distribution to determine the effect of disturbance on biotic community structure. Panel (a) represents an undisturbed community, and the data were simulated by generating random data to follow a log-normal distribution ($N = 3000$; $S = 150$). We then applied a perturbation (i.e. a disturbance event) to this community, by randomly sampling 5% of the individuals (i.e. randomly removing 95% of individuals). This resulted in a more logseries-like distribution of abundances (panel b; $N = 150$; $S = 73$). In each instance, we fit the Poisson log-normal distribution (PLN; zero-truncated version) and logseries distribution to the data and calculated the Akaike's information criterion (AIC) for the fit of each distribution. To calculate AIC, the distributions were fitted to the raw abundance data (i.e. not binned). The data were binned for graphical purposes only. The predicted values on the plots (a,b) have been generated from fitting the models to the binned data; the predicted value of the first octave from the logseries distribution has been omitted to increase clarity. In (a), the PLN clearly provides a superior fit, while in (b), the logseries has a lower AIC.

fertilization) exhibited increasingly multimodal SADs (Dornelas *et al.* 2009). A further issue relates to the fact that the SAD of a poorly sampled assemblage (i.e. a sample which represents a small proportion of the number of individuals in the assemblage) may be mistaken for a disturbed community's SAD. This is because in the situation where individuals are randomly distributed across space, small samples from log-normal-like assemblage SADs can result in truncated log-normal curve shapes (Green & Plotkin 2007). Thus, it is important to attempt to keep sampling intensity constant between the communities being studied.

In addition to analysing the fit of particular distributions, disturbance studies have focused on particular model parameters. For instance, the σ^2 parameter of the log-normal can be used to elucidate diversity information: large σ^2 means that relative abundances are spread unevenly amongst species and thus diversity is low and *vice versa*. Sæther, Engen & Grøtan (2013) showed that σ^2 significantly varied according to the level of pollution for a macro-benthos community in a Scottish lake (see also Dornelas *et al.* 2009; Tang *et al.* 2010). The α (shape) parameter of the gambin model has also been shown to be an effective metric in such circumstances (Ugland *et al.* 2007; Matthews *et al.* 2014). The gambin model is a useful SAD model in that it provides a good fit to a variety of empirical SADs, from log-normal to logseries curve shapes (Matthews *et al.* 2014). Gambin is a single parameter model, and this parameter (α) characterizes the shape of the SAD in a single value. Low values indicate logseries SAD shapes, and higher values indicate log-normal curve shapes (Ugland *et al.* 2007). As such, α may have significant potential in disturbance ecology. For instance, as described above, as a community becomes increasingly disturbed, the SAD should shift from log-normal to

logseries-like. Gambin's α provides a simple tool with which to measure this change. This process can be neatly illustrated using marine benthic invertebrate data from the EKOFISK oil field, Norway (K.I. Ugland Personal communication). The data consist of a number of unpolluted samples (average distance of 3000 m from the oil platforms) and a smaller number of highly polluted samples (100 m from the oil platforms). We have merged the unpolluted and polluted samples and plotted the SAD of each in histogram form (Fig. 2). It is clear that, as with simulated disturbance (Fig. 1), the SAD of the unpolluted sample (Fig. 2a) approximates the log-normal, while the SAD of the polluted sample (Fig. 2b) is closer to a logseries distribution. Fitting the gambin model to both data sets generates $\alpha = 2.2$ (the mean of 100 iterations of resampling the unpolluted sample to match the N of the polluted sample = 1.64), while $\alpha = 0.38$ for the polluted samples (lower, indicating curve shapes similar to a logseries distribution). This exemplifies how SAD models provide a clear and easily understood method, for example to assess the effects of disturbance on ecological communities, or to measure the impact of a particular conservation action.

Disturbance as an ecological concept is wide ranging and need not be confined to pollution. Habitat loss and fragmentation are also forms of ecological disturbance that may impact on community properties, including the SAD, which in turn may offer a rapid assessment tool (Hill *et al.* 1995; but see Nummelin 1998). The aforementioned deconstruction approach would be beneficial in this endeavour as the SAD should become more logseries-like with increasing fragmentation. However, and as with the SAR (above), an influx of generalist and matrix species into recently fragmented habitat may modify or obscure changes in the shape of the SAD.

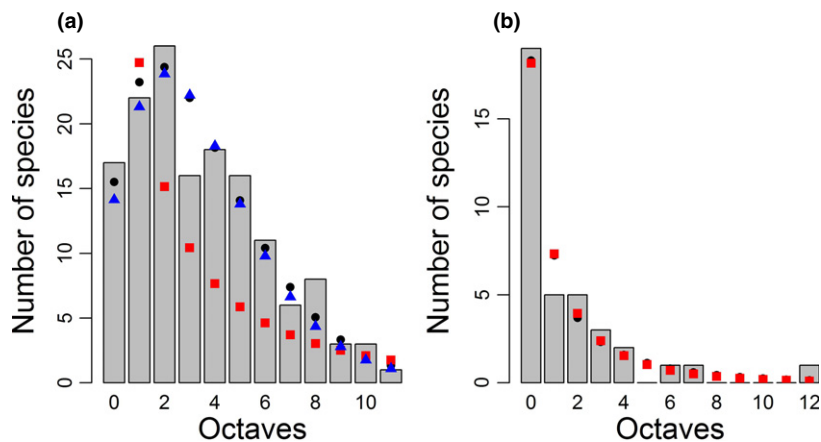


Fig. 2. The effect of pollution on a marine benthic invertebrate species abundance distribution. The data are marine benthic invertebrates from the EKOFISK oil field, Norway, and correspond to 30 unpoluted samples (average distance of 3000 m from the oil platforms) and two highly polluted samples (100 m from the oil platforms). The 30 unpoluted samples, and the two polluted samples, were merged to create (a) a single unpoluted, and (b) a single polluted, sample. The Poisson log-normal (zero-truncated; triangles), logseries (squares) and gambin (circles) distributions were fit to both sets of data (binned); the fit of the Poisson lognormal distribution to (b) is not shown as the fitting algorithm produced a warning. The α value of the unpoluted sample is 2.2 (the mean of 100 iterations of resampling the unpoluted sample to match the N of the polluted sample = 1.64), while α equals 0.38 for the polluted samples. The data were obtained from K.I. Ugland (Personal communication).

A summary of methods

Histograms are not the only method for plotting the SAD, and Fig. 3 provides a graphical summary of the various SAD methods available for examining the impact of disturbance and management actions on ecological communities. For example, Lamshead, Platt & Shaw (1983) pioneered the K dominance plot (Fig. 3a). This method plots cumulative abundance percentages against species rank and has been argued to be a useful way of determining the effect of disturbance on the SAD, but has been little explored. In K dominance plots, if a curve lies completely below another curve (as community A does in Fig. 3a), then this community can be defined as being more diverse. A similar method derived in the context of marine benthic communities uses K dominance plots to compare the distribution of individuals amongst species, with that of biomass (Fig. 3b; e.g. Warwick 1986). It is based on the theoretical consideration that the standard individual-based SAD should behave differently from the biomass-based SAD when affected by disturbance. Unpoluted systems are characterized by the biomass curve appearing above the abundance curve, as in Fig. 3b, and *vice versa*. Methods based on departures from a log-normal SAD shape (using histograms) and comparisons of model parameters (Fig. 3c,d) have been discussed above. The empirical cumulative distribution function (ECDF) can be plotted instead of the commonly used probability density function and can be useful for highlighting differences in SADs between communities (Fig. 3e). For instance, three hypothetical SADs (here, we have formulated the data ourselves for effect) are plotted in ECDF form in Fig. 3e, each relating to a river invertebrate community under different pollution scenarios: high and mildly polluted, and unpoluted. In (e), the unpoluted

curve lies below the two polluted curves at the left hand side of the plot, indicating that there are higher proportions of low abundance species in the two polluted communities. Finally, the slopes of SAD models plotted using rank abundance diagrams (RAD) offer an alternative to histograms for comparing SADs between communities (see Fig. 3f).

OTHER APPLICATIONS

Reviewing the literature reveals that SADs have been used in numerous other subfields within applied ecology, albeit sometimes sporadically. However, these uses have not been synthesized within a single review, and thus, the full potential of SAD models in applied ecology may be underappreciated. As such, we now review these different applications of SADs under five broad headings.

Conservation planning

The use of abundance data, and in particular of SADs, has significant potential in the field of conservation planning (e.g. Pearce & Ferrier 2001; Dunstan *et al.* 2012). For instance, a study by Dunstan *et al.* (2012) explored the use of SAD information in the selection of biodiversity hotspots for the benthic fish and invertebrates of the continental slope and shelf, south-west Australia. Using a novel form of rank abundance diagram (see Foster & Dunstan 2010), these authors found that incorporating SAD information greatly improved the identification of biodiversity hotspots as it provided novel information on which areas had a high proportion of rare species. The shape of RAD curves can be used to determine the proportion of relatively rare species and thus is useful for

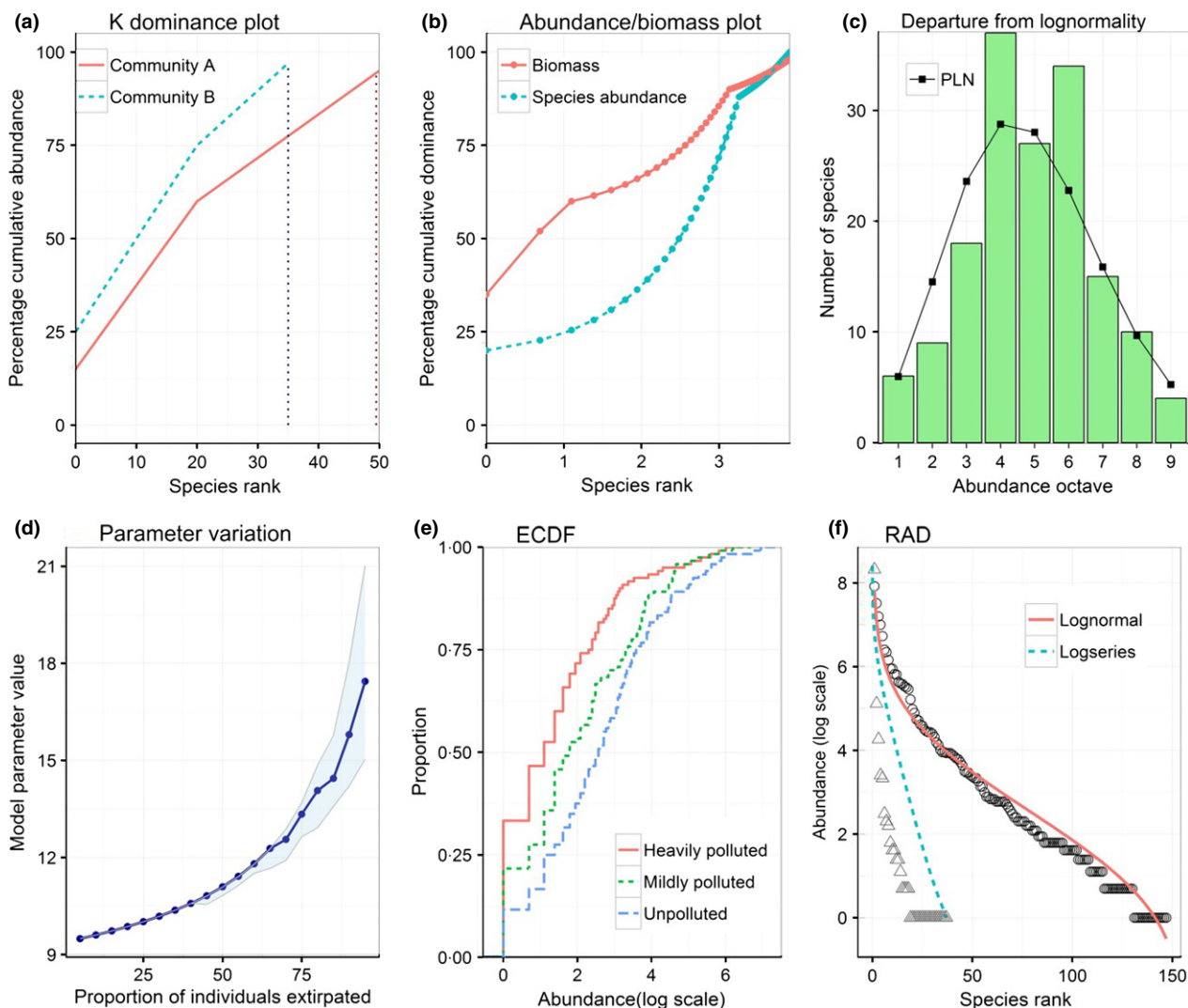


Fig. 3. Species abundance distribution-based methods for determining the effect of disturbance in applied ecology using simulated (a–e) and empirical (f) data. (a) A K dominance plot (i.e. a plot of cumulative abundance percentages against species rank; Lamshead, Platt & Shaw 1983). If a curve lies completely below another curve [as community A does in (a)], then this community can be defined as being more diverse. The vertical dashed lines in (a) indicate the species richness of each community. (b) Abundance/biomass plots (i.e. a K dominance plot that compares the distribution of individuals amongst species with that of biomass; see Warwick 1986). Unpolluted systems are characterized by the biomass curve appearing above the abundance curve, as in (b), and *vice versa*. (c) The fit of the log-normal (PLN; here, the zero-truncated form) to an empirical SAD (here, binned) is often used to assess the impact of disturbance on species assemblages. (d) Variation in the logseries alpha along a hypothetical disturbance gradient in which an increasing proportion of the individuals from a community (simulated to follow a log-normal SAD; $N = 2396$, $S = 52$) are randomly lost through sampling from the community (left to right on the x-axis represents increasing hypothetical disturbance and loss of individuals). Sampling was repeated 100 times (dots = median alpha values; shading = 95% confidence intervals). (e) Three hypothetical SADs plotted using the empirical cumulative distribution function (ECDF). The data were created for this figure in order to illustrate the method, but might for instance relate to river invertebrate communities subjected to different degrees of pollution: heavily and mildly polluted, and unpolluted. In (e), the unpolluted curve lies below the two polluted communities at the left hand side of the plot, indicating that there are a higher proportion of low abundance species in the polluted communities. (f) The SADs of the pooled polluted (triangles) and unpolluted (circles) Norwegian marine invertebrate samples (see Fig. 2. caption) are plotted in rank abundance form. The fits of the truncated log-normal model to the unpolluted samples, and the logseries model to the polluted data, are displayed. In the polluted sample, it is clear that there are more observed rare species predicted even by the logseries. The plots were constructed using the ggplot2 R package (Wickham 2009).

comparing sites and selecting necessary sites for conservation. In a further study, an analysis based on the logseries SAD predicted both the number of tree species in Amazonia and patterns of dominance and rarity (ter Steege *et al.* 2013). These striking results were of particular conservation importance as it was predicted that as many as half

the individual trees in the Amazon belong to a group of 227 ‘hyper-dominant’ species, meaning the remaining 50% of individuals are distributed across over 10 000 species. This indicates that the majority of the 10 000 species are very rare, a fact obscured when only focusing on the species richness of the region. Such findings are interesting in

themselves, but it is the general message of these papers that is most relevant in the context of this review, namely that most biodiversity conservation and land acquisition decisions are largely based on the use of species richness as an index of biodiversity (Pearce & Ferrier 2001; Dunstan *et al.* 2012), which may not reveal the whole picture. It is only when one considers the SAD of a system that any idea of the distribution of rarity and community structure can be inferred, and thus, ultimately conservation planning could be greatly improved through broader appreciation of the potential information content of SADs.

An integral part of conservation biogeography over the last 30 years has been predicting extinctions related to habitat loss and fragmentation (Whittaker & Fernández-Palacios 2007; Ladle & Whittaker 2011). This endeavour has largely centred on the backwards use of the power law SAR model, a methodology which has been criticized for being theoretically incorrect and producing erroneous extinction estimates (see Whittaker & Fernández-Palacios 2007; He & Hubbell 2011). However, recent work has shown that incorporating the SAD into extinction predictions can greatly improve the accuracy of various metrics (Kitzes & Harte 2014). For instance, the 'extinction–area relationship' and 'probabilistic species–area relationship' of Kitzes & Harte (2014) are based on the logseries SAD and upper-truncated geometric spatial abundance distribution and have been shown to be more flexible and theoretically appropriate than the power law SAR.

Finally, focusing on changes to the SAD through time is likely to provide interesting additional insights for biodiversity conservation. For instance, if we return to the area of conservation planning, it can be seen that there has been an increasing focus on temporal turnover and long-term persistence in reserve selection in the last two decades (e.g. Rodrigues, Gregory & Gaston 2000; van Teeffelen, Cabeza & Moilanen 2006). Specifically, it has been postulated that reserves and reserve networks are likely to be more successful in their aim to conserve biodiversity in the long term if the reserve sites are selected through incorporation of abundance data of any species of conservation interest (Rodrigues, Gregory & Gaston 2000). Sites should be located where these species are locally abundant, and thus, the probability of long-term persistence is higher. SADs can help in this endeavour as they give a broader perspective of relative abundances of a set of species in the network or at particular sites. For instance, theoretical work has shown that varying the assumptions on the processes affecting variations in population size through time leads to different SADs (see discussion in Sæther, Engen & Grøtan 2013).

Conservation biological control

Conservation biological control (CBC) is 'the manipulation of the environment to favour natural enemies by

either removing or mitigating adverse factors, or providing requisites that are lacking in natural enemies' habitat' (Barbosa, Caldas & Riechert 2005, p. 345). In contrast to classic biological control, which generally focuses on one or two predator–prey species interactions, CBC focuses on whole assemblages. Thus, a key aspect is analysing how abundances are distributed across different pest species and their natural enemies. In the context of CBC, Barbosa, Caldas & Riechert (2005) introduced a new method of constructing and plotting SADs called the Robbins's curve (see Fig. 4). As part of this method, incremental percentage classes of rarity or dominance (i.e. 10%, 20%, 30% up to 100%) are plotted on the x-axis, and the cumulative percentage of abundance is plotted on the y-axis. For example, the first data point along the x-axis in Fig. 4 relates to the number of individuals that belong to the rarest 10% of species and the second point to the rarest 20% and so on. The use of Robbins's curves for visualizing the SAD is beneficial as (1) the method is not biased by sample size, (2) it enables easy and accurate identification of small differences in the dominance of species, and (3) it provides a method for assessing the influence of management prescriptions on SADs, for example determining the effect of chemical pest control on the abundance of natural predators in agroecosystems (Barbosa, Caldas & Riechert 2005). Robbins' curves have rarely been applied in practice and represent an interesting avenue of future research. As we were unable to find any software for constructing a Robbins' curve, we provide the R code used to construct Fig. 4, in Appendix S1 (Supporting information).

Monitoring communities and assessing community recovery

The SAD has occasionally been employed in a monitoring capacity, for example in the monitoring of fish communities as part of fisheries management (e.g. Ambak & Mohsin 1986) and for measuring the recovery of fungi communities following managed fire disturbance (e.g. Persiani & Maggi 2013). Within such contexts, it is generally the performance of rare species that is of interest, that is rare species are the species of most conservation and management concern. Analysis of the SAD over time allows managers to observe changes in the abundance of rare species relative to the other species in the community. Studies have also examined how the SAD changes along succession gradients (e.g. Bazzaz 1975), and this type of application could easily be extended to use in forestry management. For instance, it has been shown that at the early stages of succession (e.g. following the felling of trees for timber), deciduous forest plots in Illinois, USA, exhibit a SAD that follows a geometric series, while the SAD of latter stage forest plots follow log-normal distributions (Bazzaz 1975).

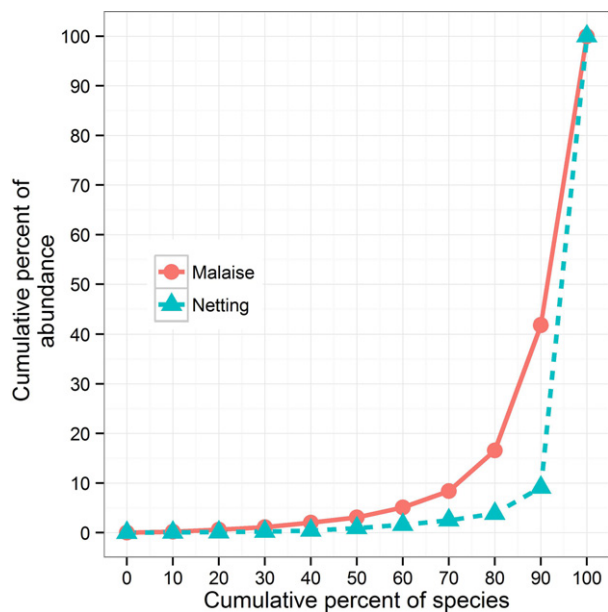


Fig. 4. Exemplar species abundance distributions plotted using the Robbins's curve method. Data are for tabanids sampled using two different methods: Malaise traps (number of species = 44) and aerial netting (number of species = 40). The data are from Tallamy, Hansens & Denno (1976; in Barbosa, Caldas & Riechert 2005). For the R code to construct the plot, see Appendix S1 (Supporting information).

Upscaling and downscaling the species abundance distribution

A large theoretical debate has ensued over the scaling properties of SADs, that is determining whether SADs can be upscaled and/or downscaled (Green & Plotkin 2007; Šizling *et al.* 2009; Borda-de-Água *et al.* 2012). The ability to accurately upscale SADs would be of great practical utility due to the economic and logistical constraints of sampling large regions and would allow for a deeper assessment of risk than just extrapolating species richness estimates over broad scales (e.g. ter Steege *et al.* 2013).

Using measures other than abundance

Almost all SAD studies use the number of individuals as the measure of abundance. However, other measures can be used, such as biomass (e.g. Anderson, Chiarucci & Williamson 2012) and resource use (e.g. Morlon *et al.* 2009). It has been shown that these different measures are not equivalent, that is individuals, biomass and resource use are not distributed amongst species in the same way (see Morlon *et al.* 2009; Henderson & Magurran 2010). Thus, focusing on SADs constructed using these other measures of abundance, or preferably focusing on all in tandem, may be a more productive way to determine the important processes driving community assembly and provides a more robust framework for examining the response of species to disturbance (Henderson & Magurran 2010). Such an approach has been little explored in

an applied context, however, with the exception of the aforementioned abundance/biomass plots (Fig. 3b; Warwick 1986). Another possibility, derived in the context of island biogeography, involves ranking species according to their incidence, that is the number of sites occupied is treated in a similar way to abundances in standard SAD models (S. Fattorini, Personal communication). A distribution of incidences can then be analysed in RAD form. This approach is based on the frequently observed positive interspecific abundance–occupancy relationship (see Gaston 1994) and may be particularly useful in fragmented landscapes where abundance data are unavailable.

Conclusions and management recommendations

Much of the recent work on SADs has placed a strong focus on the theoretical aspects of the pattern. This is a worthwhile and interesting endeavour, but we would argue that the SAD also has significant applied utility in numerous fields within ecology and biodiversity conservation. As the incidence and impact of disturbance is predicted to increase in the future (Sala *et al.* 2000), the development and use of tools that are visually intuitive, easy to implement, are applicable in a broad variety of ecological contexts and do not require substantial species-specific data is vital (Mouillot *et al.* 2013). To this end, we conclude with a set of recommendations regarding the use of SADs in applied ecological contexts:

1. When examining the effect of disturbance and management practices on biodiversity, the full SAD is a better summary of ecological community characteristics than simple diversity indices. The SAD can act as an early warning analytic for the effects of disturbance on ecological communities, as well as providing an intuitive tool for measuring the performance of ecological management prescriptions.
2. When analysing 'before and after' data (e.g. before and after a management treatment or disturbance event), plotting the SADs is beneficial as it allows the user to determine which part of the abundance spectrum (e.g. common species or rare species) is most affected by the treatment. In this regard, Figs 3 and 4 provide a useful summary of the various methods available for plotting the SAD, each providing unique information. Depending on the aim of the user, multiple plotting methods will likely provide complementary information.
3. Species abundance distribution model parameters also represent useful tools for comparing communities in a management context. For example, the α parameter of the gambin model neatly summarizes the shape of the SAD and can be used in comparative analysis and regression models.
4. Where the data allow, it can be enlightening to deconstruct the full assemblage into various subsets (e.g. based on habitat specialization) and to examine the SAD pat-

terns in the subsets separately. This enables the user, for example, to determine the impact of a specific treatment on the SAD of specialist species, these species generally being of conservation concern. Combining an assemblage deconstruction approach with the fitting of multimodal SAD models can be particularly informative in this regard.

5. Species abundance distributions have uses in applied ecology beyond the traditional applications in disturbance ecology. We have reviewed a number of such applications here (e.g. fisheries management, conservation biological control and conservation planning), and we urge workers and managers in these fields to incorporate SADs into their work.

The underlying theory, mechanisms and general properties of SADs have been heavily debated (see McGill *et al.* 2007). However, a comprehensive and unified SAD theory is not necessary for using the SAD in an applied ecological context, and there are many management situations where the SAD can provide useful information. We hope this review acts as a catalyst for a greater uptake and use of SAD-based methods in applied ecology.

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Data accessibility

Data have not been archived because this paper does not use data.

R code is provided in the Supporting Information

References

- Alonso, D., Ostling, A. & Etienne, R.S. (2008) The implicit assumption of symmetry and the species abundance distribution. *Ecology Letters*, **11**, 93–105.
- Ambak, M.A. & Mohsin, A.K.M. (1986) Monitoring population parameters for fisheries management: I. species composition, abundance and distribution patterns of fishes in Paya Bungor. *Pertanika*, **9**, 339–351.
- Anderson, B.J., Chiarucci, A. & Williamson, M. (2012) How differences in plant abundance measures produce different species-abundance distributions. *Methods in Ecology and Evolution*, **3**, 783–786.
- Barabás, G., D'Andrea, R., Rael, R., Meszéna, G. & Ostling, A. (2013) Emergent neutrality or hidden niches? *Oikos*, **122**, 1565–1572.
- Barbosa, P., Caldas, A. & Riechert, S.E. (2005) Species abundance distribution and predator-prey interactions. *Ecology of Predator-Prey Interactions* (eds P. Barbosa & I. Castellanos), pp. 344–369. Oxford University Press, New York.
- Bazzaz, F.A. (1975) Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecology*, **56**, 485–488.
- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I. & Öckinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 2075–2082.
- Borda-de-Água, L., Borges, P.A.V., Hubbell, S.P. & Pereira, H.M. (2012) Spatial scaling of species abundance distributions. *Ecography*, **35**, 549–556.
- Borges, P.A.V., Ugland, K.I., Dinis, F.O. & Gaspar, C.S. (2008) Insect and spider rarity in an oceanic island (Terceira, Azores): True rare and pseudo-rare species. *Insect Ecology and Conservation* (ed. S. Fattorini), pp. 47–70. Research Signpost, Kerala.
- Dornelas, M. & Connolly, S.R. (2008) Multiple modes in a coral species abundance distribution. *Ecology Letters*, **11**, 1008–1016.
- Dornelas, M., Soykan, C.U. & Ugland, K.I. (2011) Biodiversity and disturbance. *Biological Diversity: Frontiers in Measurement and Assessment* (eds A.E. Magurran & B.J. McGill), pp. 237–251. Oxford University Press, Oxford.
- Dornelas, M., Moonen, A.C., Magurran, A.E. & Bärberi, P. (2009) Species abundance distributions reveal environmental heterogeneity in modified landscapes. *Journal of Applied Ecology*, **46**, 666–672.
- Dunstan, P.K., Bax, N.J., Foster, S.D., Williams, A. & Althaus, F. (2012) Identifying hotspots for biodiversity management using rank abundance distributions. *Diversity and Distributions*, **18**, 22–32.
- Fattorini, S. (2005) A simple method to fit geometric series and broken stick models in community ecology and island biogeography. *Acta Oecologica*, **28**, 199–205.
- 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 of an animal population. *Journal of Animal Ecology*, **12**, 42–58.
- Foster, S.D. & Dunstan, P.K. (2010) The analysis of biodiversity using rank abundance distributions. *Biometrics*, **66**, 186–195.
- Gaston, K.J. (1994) *Rarity*. Springer, The Netherlands.
- Gray, J.S., Bjørgseter, A. & Ugland, K.I. (2005) The impact of rare species on natural assemblages. *Journal of Animal Ecology*, **74**, 1131–1139.
- Gray, J.S., Bjørgseter, A. & Ugland, K.I. (2006) On plotting species abundance distributions. *Journal of Animal Ecology*, **75**, 752–756.
- Gray, J.S. & Mirza, F.B. (1979) A possible method for the detection of pollution-induced disturbance on marine benthic communities. *Marine Pollution Bulletin*, **10**, 142–146.
- Gray, J.S., Waldichuk, M., Newton, A.J., Berry, R.J., Holden, A.V. & Pearson, T.H. (1979) Pollution-induced changes in populations. *Philosophical Transactions of the Royal Society of London B, Biological Sciences*, **286**, 545–561.
- Green, J.L. & Plotkin, J.B. (2007) A statistical theory for sampling species abundances. *Ecology Letters*, **10**, 1037–1045.
- Hågvar, S. (1994) Log-normal distribution of dominance as an indicator of stressed soil microarthropod communities? *Acta Zoologica Fennica*, **195**, 71–80.
- He, F. & Hubbell, S.P. (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature*, **473**, 368–371.
- Henderson, P.A. & Magurran, A.E. (2010) Linking species abundance distributions in numerical abundance and biomass through simple assumptions about community structure. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 1561–1570.
- Hill, J.K., Hamer, K.C., Lace, K.C. & Banham, W.M.T. (1995) Effects of selective logging on tropical forest butterflies on Buru, Indonesia. *Journal of Applied Ecology*, **32**, 754–760.
- Kim, D.-H., Cho, W.-S. & Chon, T.-S. (2013) Self-organizing map and species abundance distribution of stream benthic macroinvertebrates in revealing community patterns in different seasons. *Ecological Informatics*, **17**, 14–29.
- Kitzes, J. & Harte, J. (2014) Beyond the species–area relationship: improving macroecological extinction estimates. *Methods in Ecology and Evolution*, **5**, 1–8.
- Kürka, P., Şizling, A.L. & Rosindell, J. (2010) Analytical evidence for scale-invariance in the shape of species abundance distributions. *Mathematical Biosciences*, **223**, 151–159.
- Labra, F.A., Abades, S.R. & Marquet, P.A. (2005) Distribution and abundance: scaling patterns in exotic and native bird species. *Species Invasions: Insights Into Ecology, Evolution, and Biogeography* (eds D.F. Sax, J.J. Stachowicz & S.D. Gaines). Pp. 421–446. Sinauer, Sunderland, MA.
- Ladle, R.J. & Whittaker, R.J. (eds.) (2011) *Conservation Biogeography*. Wiley-Blackwell, Chichester.
- Lambhead, 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. *Journal of Natural History*, **17**, 859–874.
- Magurran, A.E. (2004) *Measuring Biological Diversity*, 2nd edn. Blackwell, Oxford.
- Magurran, A.E. & Henderson, P.A. (2003) Explaining the excess of rare species in natural species abundance distributions. *Nature*, **422**, 714–716.

- Marquet, P.A., Fernández, M., Navarrete, S.A. & Valdovinos, C. (2004) Diversity emerging: toward a deconstruction of biodiversity patterns. *Frontiers of Biogeography: New Directions in the Geography of Nature* (eds M.V. Lomolino & L.R. Heaney), pp. 191–209. Sinauer, Sunderland, MA.
- Matthews, T.J., Borregaard, M.K., Ugland, K.I., Borges, P.A.V., Rigal, F., Cardoso, P. & Whittaker, R.J. (2014) The gambin model provides a superior fit to species abundance distributions with a single free parameter: evidence, implementation and interpretation. *Ecography*, doi:10.1111/ecog.00861.
- Matthews, T.J., Borges, P.A.V. & Whittaker, R.J. (2014) Multimodal species abundance distributions: a deconstruction approach reveals the processes behind the pattern. *Oikos*, **123**, 533–544.
- Matthews, T.J., Cottee-Jones, H.E.W. & Whittaker, R.J. (2014) Habitat fragmentation and the species–area relationship: a focus on total species richness obscures the impact of habitat loss on habitat specialists. *Diversity and Distributions*, doi:10.1111/ddi.12227.
- Matthews, T.J. & Whittaker, R.J. (2014) Fitting and comparing competing models of the species abundance distribution: assessment and prospect. *Frontiers of Biogeography*, **6**, 67–82.
- May, R.M. (1975) Patterns of species abundance and diversity. *Ecology and Evolution of Communities* (eds M.L. Cody & J.M. Diamond), pp. 81–120. Harvard University Press, Cambridge, MA.
- McGill, B.J. (2011) Species abundance distributions. *Biological Diversity: Frontiers in Measurement and Assessment* (eds A.E. Magurran & B.J. McGill), pp. 105–122. Oxford University Press, Oxford.
- McGill, B.J., Etienne, R.S., Gray, J.S., Alonso, D., Anderson, M.J. & Benecha, H.K. *et al.* (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, **10**, 995–1015.
- Morlon, H., White, E.P., Etienne, R.S., Green, J.L., Ostling, A. & Alonso, D. *et al.* (2009) Taking species abundance distributions beyond individuals. *Ecology Letters*, **12**, 488–501.
- Moullot, D. & Lepretre, A. (2000) Introduction of relative abundance distribution (RAD) indices, estimated from the rank-frequency diagrams (RFD), to assess changes in community diversity. *Environmental Monitoring and Assessment*, **63**, 279–295.
- Moullot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H. & Bellwood, D.R. (2013) A functional approach reveals community responses to disturbances. *Trends in Ecology & Evolution*, **28**, 167–177.
- Newman, E.I. (1993) *Applied Ecology*. Blackwell Scientific Publications, Oxford.
- Nummelin, M. (1998) Log-normal distribution of species abundances is not a universal indicator of rain forest disturbance. *Journal of Applied Ecology*, **35**, 454–457.
- Pearce, J. & Ferrier, S. (2001) The practical value of modelling relative abundance of species for regional conservation planning: a case study. *Biological Conservation*, **98**, 33–43.
- Persiani, A.M. & Maggi, O. (2013) Species-abundance distribution patterns of soil fungi: contribution to the ecological understanding of their response to experimental fire in Mediterranean maquis (southern Italy). *Mycologia*, **105**, 260–276.
- Pielou, E.C. (1969) *An Introduction to Mathematical Ecology*. John Wiley & Sons, New York.
- Preston, F.W. (1948) The commonness, and rarity, of species. *Ecology*, **29**, 254–283.
- Rodrigues, A.S.L., Gregory, R.D. & Gaston, K.J. (2000) Robustness of reserve selection procedures under temporal species turnover. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **267**, 49–55.
- Sæther, B.-E., Engen, S. & Grøtan, V. (2013) Species diversity and community similarity in fluctuating environments: parametric approaches using species abundance distributions. *Journal of Animal Ecology*, **82**, 721–738.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J., Berlow, E., Bloomfield, J. & Dirzo, R. *et al.* (2000) Global biodiversity scenarios for the year 2100. *Science*, **287**, 1770–1774.
- Šizling, A., Storch, D., Reif, J. & Gaston, K. (2009) Invariance in species-abundance distributions. *Theoretical Ecology*, **2**, 89–103.
- ter Steege, H., Pitman, N.C.A., Sabatier, D., Baraloto, C., Salomão, R.P. & Guevara, J.E. *et al.* (2013) Hyperdominance in the Amazonian tree flora. *Science*, **342**, 1243092.
- Syrek, D., Weiner, W.M., Wojtylak, M., Olszowska, G. & Kwapis, Z. (2006) Species abundance distribution of collembolan communities in forest soils polluted with heavy metals. *Applied Soil Ecology*, **31**, 239–250.
- Tallamy, D.W., Hansens, E.J. & Denno, R.F. (1976) Comparison of malaise trapping and aerial netting for sampling a horsefly and deerfly community. *Environmental Entomology*, **5**, 788–792.
- Tang, H., Song, M.-Y., Cho, W.-S., Park, Y.-S. & Chon, T.-S. (2010) Species abundance distribution of benthic chironomids and other macroinvertebrates across different levels of pollution in streams. *International Journal of Limnology*, **46**, 53–66.
- van Teeffelen, A.J.A., Cabeza, M. & Moilanen, A. (2006) Connectivity, probabilities and persistence: comparing reserve selection strategies. *Biodiversity & Conservation*, **15**, 899–919.
- Tokeshi, M. (1993) Species abundance patterns and community structure. *Advances in Ecological Research*, **24**, 111–186.
- Ugland, K.I. & Gray, J.S. (1982) Lognormal distributions and the concept of community equilibrium. *Oikos*, **39**, 171–178.
- Ugland, K.I., Lamshead, P.J.D., McGill, B., Gray, J.S., O’Dea, N., Ladle, R.J. & Whittaker, R.J. (2007) Modelling dimensionality in species abundance distributions: description and evaluation of the Gambin model. *Evolutionary Ecology Research*, **9**, 313–324.
- Ulrich, W. & Zalewski, M. (2006) Abundance and co-occurrence patterns of core and satellite species of ground beetles on small lake islands. *Oikos*, **114**, 338–348.
- Unterseher, M., Jumpponen, A.R.I., Öpik, M., Tedersoo, L., Moora, M., Dormann, C.F. & Schnittler, M. (2011) Species abundance distributions and richness estimations in fungal metagenomics – lessons learned from community ecology. *Molecular Ecology*, **20**, 275–285.
- Vergnon, R., van Nes, E.H. & Scheffer, M. (2012) Emergent neutrality leads to multimodal species abundance distributions. *Nature Communications*, **3**, 663.
- Warwick, R.M. (1986) A new method for detecting pollution effects on marine macrobenthic communities. *Marine Biology*, **92**, 557–562.
- Whittaker, R.J. & Fernández-Palacios, J.M. (2007) *Island Biogeography: Ecology, Evolution, and Conservation*, 2nd edn. Oxford University Press, Oxford.
- Wickham, H. (2009) *Ggplot2: Elegant Graphics for Data Analysis*. Springer, New York.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. R code to construct the Robbins’s curve.