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REVIEW

Species and trait abundance distributions as tools for understanding disturbance effects and community assembly in applied ecology

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[Correction added on 5 September 2025, after first online publication: The ORCID for Paulo V. A. Borges has been corrected.]

Abstract

1. Species abundance distributions (SADs) depict the order of species based on their ranked abundances. While they have been central to much theoretical work in community ecology, their practical value in applied ecology is still debated.
2. Supported by a meta-analysis of 1153 publications on SADs, we review the state of the art in the practical use of SADs and provide a conceptual framework for the study of SADs in an applied context.
3. Of the studies sourced through the meta-analysis, only 5% had a truly applied focus; 93% of these studies dealt with the influence of agricultural practices, forest management, pollution or other forms of disturbance on the shape of the SAD.
4. We found little support for previous claims that disturbance shifts species abundance distributions from a lognormal to a steep logseries form. Some species-rich communities, such as tropical forests, are well fit by a logseries even in the absence of disturbance, and steep, uneven SADs may be more representative of dispersal-limited communities under neutral dynamics.
5. *Policy implications*. Further insight into the links between disturbance and species abundance may come from the recognition that the species abundance distribution (SAD) is a special case of a broader concept, the trait abundance distribution (TAD), which can provide indirect information on resource utilisation and niche partitioning. An analysis of the changes in SADs and TADs, together with environmental data, should allow for a better understanding of the assembly and functioning of ecological communities in both applied and basic ecology.

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KEYWORDS
community functioning, disturbance, dominance, functional traits, lognormal distribution, logseries distribution, species rank order

1 | SADS IN APPLIED ECOLOGY

1.1 | The concept and use of species abundance distributions

The species abundance distribution (SAD) has inspired ecologists since the pioneering work of Motomura (1932), Fisher et al. (1943) and Preston (1948). SADs, which describe the (relative) abundance of all species recorded within a sampled assemblage, contain the basic information about species richness, diversity and evenness (Magurran, 2013). They reflect the dominance order of species, a pattern generated by multiple processes including population dynamics, environmental conditions, species interactions, resource use and/or stochastic processes (Dornelas et al., 2009; Hubbell, 2001; May, 1975; McGill et al., 2007; Morlon et al., 2009). Here, we use the term SAD to denote the order of species ranks according to their (relative) abundance (Whittaker, 1965). This type of representation of the SAD, often described as a rank abundance (i.e. RAD or Whittaker plot), does not lose information from abundance binning and allows for the identification of the contribution of individual species.

The study of SADs has primarily focused on three different approaches depicted in the conceptual Figure 1. First, numerous studies have approached SADs from a theoretical perspective (explanatory approaches in Figure 1), trying to understand observed distributions either through the use of niche-based models (reviewed in Tokeshi, 2009), individual-based neutral models (e.g. Hubbell, 2001) and population dynamic models (e.g. Engen & Lande, 1996), or by mimicking SAD shapes using different statistical distributions (Fisher et al., 1943; May, 1975; Preston, 1948; Ulrich et al., 2018). So far, theoretical work on SADs has arguably resulted in limited mechanistic ecological insight, as different models (often with contrasting underlying assumptions) can generate very similar SADs that match those observed in empirical systems (McGill, 2010). Although not all theories erected to explain SADs are comparable in terms of their efficiency and/or first

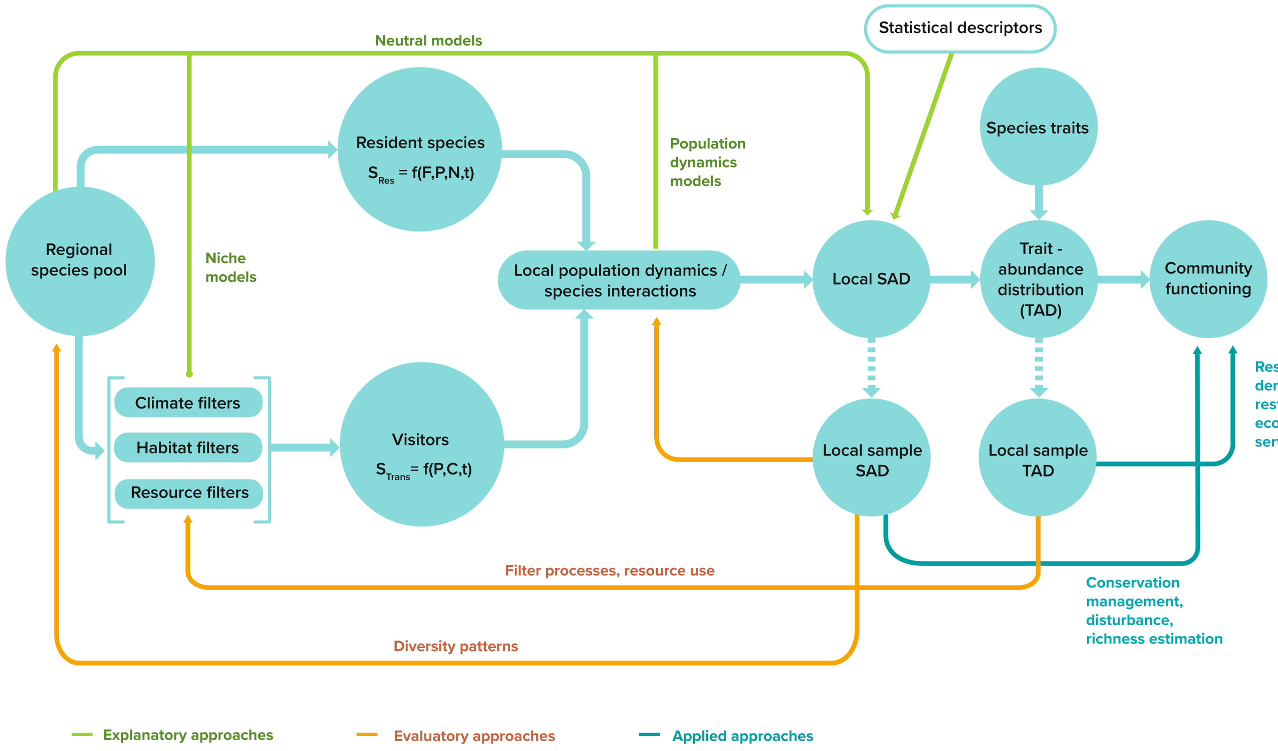

FIGURE 1 Conceptual framework of how to study species abundance (SAD) and species trait abundance (TAD) distributions from three differences perspectives: Explanatory (green), evaluator (orange) and applied (blue). Explanatory approaches seek to understand specific SAD shapes and diversity patterns from processes at the population level (dispersal, population dynamics and extinction), evaluatory approaches use the SAD, for example, richness forecasting and filter effects. Applied approaches, for example, the assessment of ecosystem services or habitat management, require information about species traits. Resident species richness (S_{Res}) is assumed to be a function of filtering effects (F), species pool richness (P), pool abundance (N) and time (*t*). Visitor species richness (S_{Trans}) is a function of pool richness, colonisation potential (C) and time (*t*).

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principles and epistemic status (Marquet et al., 2014), the fact that very different ecological processes can converge into the same few SAD shapes might provide information about the constraints on the assembly and persistence of communities, a fact that has received comparatively little attention. In this respect, Locey and White (2013) demonstrated how abundance, and richness itself, constrain the form of SADs, while Allesina and Tang (2012) and Ulrich et al. (2020) identified stability criteria and areas of SAD parameter space not realised in nature, specifically very unevenly and highly evenly distributed communities. Diaz et al. (2021) made progress in explaining some of these results, with the finding that empirical SADs are more uneven than expected by chance, pointing to additional selective forces that act on species dominance or to processes that allow very rare species to persist.

Second, the evaluatory approach has also been frequently used to study SADs (Figure 1), with observed SADs being used to estimate the species richness of species pools (ter Steege et al., 2013, 2020; Ulrich & Ollik, 2005), to evaluate temporal dynamics (Solbu et al., 2022) and to assess community assembly (Fattorini et al., 2016; Nemergut et al., 2013). With regard to the latter, a common approach is to determine how different predictor variables (e.g. island area and isolation, storm frequency, temperature and elevation) affect parameters of the SAD (Ibanez et al., 2020; Matthews et al., 2017, 2019; Ulrich et al., 2022; Yen et al., 2013). The evaluatory approach to SADs has also involved the integration of species traits (e.g. Koffel et al., 2022).

Far fewer studies have focused on the third approach depicted in Figure 1: the use of the SAD in applied ecology (Matthews & Whittaker, 2015). Most often, SADs have been used to estimate local species richness (e.g. Autio et al., 2013; Borda-de-Água, 2019; Fagan & Kareiva, 1997; Terra et al., 2017). Various authors have highlighted the potential importance of SAD modelling for evaluating the impact of anthropogenic disturbance (e.g. Dornelas et al., 2009; Kim et al., 2013) and to predict species extinction risk (Kitzes & Harte, 2015). Applied SAD studies based on empirical data remain limited and often assume that undisturbed systems should follow lognormal SADs (May, 1975; Preston, 1948; Ugland & Gray, 1982). Disturbance or high levels of dispersal are thought to shift SADs towards more pronounced dominance patterns, as mimicked by the logseries (Hill & Hamer, 1998; Matthews & Whittaker, 2015; Preston, 1980). Specifically, a common assumption is that well-balanced ecosystems support species with more varied ecological niches and hence have stable populations of core species with moderate to large numbers of individuals (Hooper et al., 2005; Turnbull et al., 2016). In line with May's (1975) arguments related to the central limit theorem, multiple ecological factors in closed communities should lead to SADs being well approximated by lognormal distributions (Magurran & Henderson, 2003). In contrast, open communities and those subject to stressful conditions are expected to have higher species dominance and hence deviate substantially from this pattern, approaching a logseries (Gray et al., 1997; Gray & Mirza, 1979). However, there are several shortcomings with this approach. First, even in high diversity systems such as tree communities in tropical forests, local and regional 'undisturbed' communities can follow a logseries (ter Steege et al., 2013, 2020). Thus, adherence of an empirical SAD to a particular model may not be particularly informative about ecosystem status. Indeed, the comprehensive review of Baldridge et al. (2016) of more than 16,000 empirical SADs found the logseries to provide the best fit in most cases, while Alroy (2015) reported common shapes intermediate between logseries and lognormal. However, neither study linked model performance to environmental conditions, sample coverage or differences in the importance of dispersal. Second, some studies have shown that disturbance can cause a shift from a lognormal to a logseries-like SAD (or other SAD shapes), but with further disturbance driving a shift back to a more lognormal SAD shape (perhaps with different parameters to the original) (Gray & Mirza, 1979; Hågvar, 1994; Matthews & Whittaker, 2015). Nonetheless, while there may not be a general pattern of shift in SAD shape in response to disturbance, it has been frequently shown that dominance structures and therefore SADs are sensitive to disturbance (and arguably more so than many commonly used diversity metrics) and thus represent a potentially useful tool in the applied ecologist's tool kit (Dornelas et al., 2009; Gray & Mirza, 1979; Hill & Hamer, 1998; Matthews & Whittaker, 2015), as well as in that of epidemiologists (Izsák, 2005). However, to date, no critical analysis has been published that assesses how SADs have been used in applied ecology and the insights that have been gained by this use.

The most recent review of the SAD in an applied context was published 10 years ago by Matthews and Whittaker (2015). Their review showed that, up to that time, applied studies using SADs were mainly based on the aforementioned assumption that niche-based community assembly leads to lognormal SADs, with authors trying to identify how different anthropogenic disturbance regimes, particularly pollution, affected SAD shapes (e.g. Dornelas et al., 2009; Gray & Mirza, 1979). However, there have been numerous recent developments in SAD research of relevance to applied ecology. These include the incorporation of functional traits into the study of the SAD (Li et al., 2021) and the maximum entropy model of ecology and its extensions (METE). METE makes predictions regarding the SAD and has been used, for example, to assess the impacts of land use change on biodiversity (Brush et al., 2022; Brush & Harte, 2021; Harte et al., 2021; Newman et al., 2020). As such, a decade after the review of Matthews and Whittaker (2015) it seems necessary to reapproach the topic, to widen the scope, and to review what has been achieved in the intervening 10 years.

The aim of the present review was to assess whether SADs are indeed a useful tool in applied ecology or whether they are merely of theoretical interest. To achieve this, we draw on the large theoretical and empirical literature on SADs to first discuss which types of SAD are expected under equilibrium and disturbance conditions, thus providing the theoretical context in which applied SAD research is grounded. We then survey the literature to obtain an overview of how SADs have been used in applied ecological

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studies, evaluating the findings in relation to established theories. Based on these two steps, going forward we advocate the importance of formulating a general framework for the usage of SADs in applied ecology that integrates information on species traits. This is particularly important because many applied SAD studies rely on theoretical assumptions about SAD behaviour that still require empirical confirmation. To help meet this goal, we highlight that the trait abundance distribution (TAD) might serve as a tool to obtain insights into the effects of environmental disturbances on the dominance structure of ecological communities. While previous studies have analysed the TAD, few have used the SAD and TAD in combination to derive applied ecological insights (e.g. Koffel et al., 2022). We note that other approaches have been proposed to aid in the understanding of disturbance on ecological communities, such as the CATs (community assembly via trait selection) approach that was developed in the context of maximum entropy theory and population dynamics (Shipley et al., 2006; Warton et al., 2015). However, these approaches are primarily community focused and are based on specific assumptions related, for example, to dispersal and growth dynamics. Our proposed approach, which involves the direct comparison of SADs and TADs, is more species-focused and its use does not rely on any a priori assumptions.

2 | EXPECTED TYPES OF SADS UNDER EQUILIBRIUM AND DISTURBANCE REGIMES

2.1 | Expected equilibrium SAD shapes

To understand, and effectively measure, how SADs respond to disturbance, it is useful to have a good understanding of the SADs of undisturbed communities at equilibrium. In this respect, neutral ecological models provide some insight (Etienne & Olff, 2005; Harte, 2011; Hubbell, 2001; Matthews & Whittaker, 2014). The maximum entropy model (METE) predicts a logseries at equilibrium irrespective of boundary conditions (Bowler, 2014; Harte, 2011). The zero sum multinomial SAD model (ZSM), based on a spatially implicit neutral model (with a local community and a larger associated source pool), explicitly assumes species ecological equivalence and predicts that the major trigger of the shape of local SADs is the amount of dispersal limitation and dispersal into a community (Hubbell, 2001). In the spatially explicit version of the model, dispersal also fully determines the degree of isolation of a community. In a not fully neutral context, isolation can be associated with the strength of habitat filters and, therefore, habitat conditions (Jabot et al., 2008). High isolation (i.e. low dispersal into the local community) drives ZSM communities to monodominance of a single species, while moderate dispersal or any deviation from the assumptions of neutral theory regarding species equivalence might lead to diverse, stable communities. Such deviations include differential recruitment (Zhou & Zhang, 2008) or intransitive competitive interactions (Ulrich et al., 2017). Some communities of intermediate dispersal limitation tend to follow lognormal-like SADs (Etienne & Olff, 2005; Matthews & Whittaker, 2014). In turn and irrespective of the specific type of neutral model, high or even unlimited dispersal generates communities with a relatively higher number of rare species and pronounced dominance order, resulting in SADs that follow a logseries-like distribution (Hubbell, 2001). Thus, neutral models provide a null expectation about abundance distributions under differential dispersal. In extended neutral models, the lognormal—logseries gradient is expected to reflect the degree of isolation or habitat filtering in a community (Jabot & Chave, 2011). However, to be of practical value, information on the average strength of dispersal or of selective filtering is a necessary minimum requirement. This information might be obtained from diffusion models of population dynamics where the parameters reflect the relative contribution of immigration and local extinction on the relative abundance of species (Marquet et al., 2017).

Dispersal is also the driver behind the core-satellite model of species occupancy (Hanski, 1982). Communities dominated by a group of core species, which are permanent community members, are theorised to be assembled by species interactions and ecological filters based on niche differentiation. The multiplicative interplay of many such mechanisms would generate lognormal distributions (Magurran & Henderson, 2003; May, 1975). In contrast, communities dominated by transient (satellite) species that are characterised by high colonisation/extinction rates should exhibit logseries shapes, as predicted by neutral models (Magurran & Henderson, 2003). Many communities will be combinations of core and transient species, and in such cases, depending on the relative proportion of each group, we may expect SAD shapes with or without an excess of rare species (Moradi et al., 2025). It is likely that anthropogenic disturbance will alter the proportions of core and transient species in a given community, thus also affecting the form of the SAD, although exactly how is difficult to predict. For example, light disturbance might simply increase the number of transient species (e.g. species associated with human land-uses in the wider landscape habitat matrix; Matthews, 2021), while heavy disturbance could lead to the replacement of the original core species with a new set of core species better adapted to the disturbed conditions (Gray & Mirza, 1979).

These core and satellite species groups are often seen to relate to the endpoints of a niche–neutral continuum that is governed partly by the degree of dispersal (Fargione et al., 2003; Fisher & Mehta, 2014). As such, it is not surprising that a multitude of mixed neutral—niche-based SAD models have been proposed (e.g. Alroy, 2015; Ulrich et al., 2017). Again, evidence for this niche–dispersal scenario remains mixed, likely in part because it is often difficult to assess the relative importance of both mechanisms; even small uncertainty in the measurement of the true impacts of both factors might return questionable results. Further, simulations have shown that even very high sample sizes may be insufficient to discern between these two mechanisms through analysis of the SAD alone (Hammal et al., 2015). To understand, and effectively measure,

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how SADs respond to disturbance, we should have a better understanding of the SADs of undisturbed communities at equilibrium.

2.2 | Disturbance and the SAD

How might disturbance affect community processes and therefore species relative abundances? To provide insights into this question, we adopted a simulation approach and considered a resampling model (Figure 2). Under the assumption that disturbance affects species abundances or even eliminates species from the local community, we can predict changes in SAD shape after disturbance. Higher probabilities of elimination or reduction of relatively rare species are predicted to transform an initial lognormal SAD into one that common fitting routines would not distinguish from a logseries (Figure 2c). Even equiprobable decline along the dominance order or preferential decline of abundant species can lead to SADs similar in shape to the logseries (Figure 2b,d). In turn, an initial logseries SAD remains logseries-like in the majority of disturbance regimes (Figure 2f–i). Only moderate abundance fluctuations, as for instance realised by a random walk, might transform a logseries into a shape similar to a lognormal distribution (Figure 2f). Importantly, except for the case of predominant elimination of rare species, disturbance tends to increase evenness in the examples of Figure 2. We note that our simple simulation does not refer to specific types of disturbance. A detailed mapping of the many different disturbance regimes and their observed or hypothesised influences on species abundances is still missing and is a priority for future applied SAD research. Such a mapping is needed to constrain the many possible links between disturbance, dominance order and SAD shape.

Using this resampling model, we can infer how different disturbance regimes and applied ecological models are related to SAD shapes. For example, Dornelas (2010) developed a mortality—carrying capacity—reproduction classification model of the consequences of disturbance that has implications for the shape of the SAD. In particular, the model implies that disturbance might remove or replace local habitat filters (Barrett et al., 2023; Smith et al., 2022). This might lead to increased immigration with or without local species elimination and, under the neutral perspective, to higher dispersal rates and a shift towards logseries SADs (exemplified in Figure 2a,c,d). For example, Myers and Harms (2009) reported increased seed arrival and local plant richness after disturbance in a wide range of

FIGURE 2 Seven simplified resampling models to exemplify possible effects of disturbance on the shape of the SAD. Two pre-disturbance SAD shapes are shown: Lognormal and logseries distributions. For each pre-disturbance SAD, a set of five disturbance scenarios was simulated with stochastic abundance fluctuations of different strength. In each case, Pielou evenness values $E = e^{H}/S$ for each SAD are provided, with H being the Shannon diversity and S the number of species. (a, f) Moderate (orange SAD) and strong (green SAD) stochastic abundance fluctuations generate SADs often having an excess of rare species, and a loss of species when abundances of some species fall below an assumed extinction threshold (green SAD). (b, g) Equiprobable random elimination of species irrespective of abundance retains the general SAD form (orange). Equiprobable random elimination of individuals forces the pre-disturbance lognormal SAD into a logseries shape (b), but with fewer species (green), while the pre-disturbance logseries SAD is relatively unchanged (g). (c, h) Higher probabilities of the elimination of rare species (orange) or individuals from rarer species (green) force pre-disturbance lognormal SADs into a logseries shape. Increased dispersal (dashed line) further enhances the logseries shift. (d, i) In rare cases, disturbance might eliminate (orange) or reduce (green) the abundance of the relatively more abundant species. This increases evenness and retains the logseries shape. Increased dispersal again shifts the lognormal into a logseries shape (orange dashed line). (e, j) If the process of species elimination and population decreases are trait dependent, the specific combination of species traits in a community determines the resulting SAD shape, and no predictions can be made if only SAD data are available. SAD, species abundance distribution.

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habitat types, although these authors did not report effects on SAD shapes explicitly. Similarly, Riffo-Donoso et al. (2021) reported increased species turnover in bryophyte communities after anthropogenic disturbance in temperate forests. However, disturbance might also act as an additional filter, with this decreasing dispersal (Fraaije et al., 2015). Therefore, the specific change in SAD form strongly depends on the specific disturbance regime.

Disturbance might alter population dynamics in the community with or without immediate species loss (Keen et al., 2021; McMullen et al., 2017). If the post-disturbance variability in population size remains proportional to the pre-disturbance one, average relative abundance should remain unaffected. In most other cases, relative abundances and also the SAD shape would change, although not necessarily in the direction of a logseries (Figure 2a). The exact changes would depend on the scaling properties of specific SADs and these are still not well understood (Antão et al., 2021; de Lima et al., 2020; Enquist et al., 2019; Green & Plotkin, 2007; Ulrich et al., 2022). If disturbance is associated with species loss (Figure 2b–d), we might assume that rarer species are more prone to vanish in such situations (Horváth et al., 2019; O'Grady et al., 2004; Smith & Almeida, 2020). In such cases, an initial lognormal SAD might preferentially lose species in its lower tail of rarest species, making the SAD similar to a logseries (Figure 2c). However, cases are known where survival probabilities after disturbance appeared to be independent of abundance (Trubovitz et al., 2023). In such cases, no predictions about the SAD can be made without knowledge of the species-specific extinction probabilities. Overall, these simple simulations highlight the difficulties in inferring the influence of disturbance from changes in the shape of the SAD alone.

3 | QUANTIFYING THE USE OF SADS IN APPLIED ECOLOGY

We retrieved 1153 documents, mainly scientific publications from various internet sources, that potentially used SADs in applied ecological research. Details on the search strategy, the sources and keywords are provided in Appendix S1. After manual screening, the vast majority appeared to deal with the explanatory (694) and evaluatory (586; with overlap between both categories) approaches to SADs as outlined in Figure 1. Only 64 publications explicitly referred to the applied approach according to Figure 1 (references in Appendix S1). The 64 case studies sourced through our literature search cover different biomes (marine, freshwater and terrestrial) and habitat types, and include a diversity of taxa (4 bacteria/plankton, 21 plant, 22 arthropod, 5 fish, 2 reptile, 3 bird and 1 mammal study, and 6 studies covering multiple taxa). We note, however, that our search strategy may have missed a large part of the grey literature on SAD applications, such as unpublished expert opinions, management reports and other material not freely available. We also did not include work that used derived measures of abundance, such as various diversity and evenness metrics, or richness estimators. Overall, we retrieved remarkably few studies given the frequent assertions about the usefulness of SADs in applied ecology (e.g. Matthews & Whittaker, 2015; McGill et al., 2007).

Of the 64 sourced studies, a large number (30 studies) focused on the distinction between lognormal and logseries shaped SADs, and 32 of them aimed to assess the degree of habitat disturbance or environmental stress on some measure of SAD form (Figure 3). Importantly, 16 publications reported a link between lognormal SADs and natural, undisturbed conditions, while 11 papers did not find clear evidence for this assumption (Figure 3). In turn, only two studies with three datasets (Lin et al., 2016; Remadevi et al., 2023) linked the logseries to natural conditions. This distribution within our dataset is surprising as a number of previous papers found natural and undisturbed, particularly tropical, communities to follow logseries SADs (Hubbell et al., 2008; ter Steege et al., 2020; Ulrich et al., 2010). Ulrich et al. (2016) reported comparatively extreme conditions to be associated with lognormal SADs in global drylands. The findings of Gray and Mirza (1979) and Hågvar (1994) on marine benthic and terrestrial soil communities also point to shifts from lognormal to logseries distributions under disturbance, where a lognormal might reappear under extreme stress. These latter findings would fit into the assumption that niche-based processes within the group of specialised core species adapted to harsh conditions lead to lognormal shaped SADs. Only Mason et al. (2008) referred to a trait-based approach to SADs in a study on lacustrine fish communities and concluded that common and rare species differ in the relative degree of niche overlap.

Our review of the applied SAD literature reveals that (i) there are fewer applied ecological studies utilising SADs than expected given the number of studies that have argued for their utility in such contexts, and (ii) those applied studies that have used SADs have had varying degrees of success, often employing SAD models in different ways and based on varying underlying theoretical assumptions.

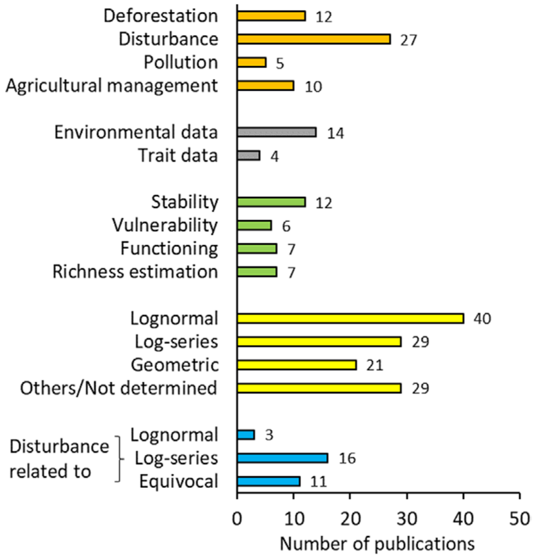

FIGURE 3 Summary statistics for 64 publications on SAD application. Note that categories can overlap. SAD, species abundance distribution.

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Given these findings, it is thus necessary to ask why this is the case and what can be done to improve the usefulness of SADs in applied ecology?

For SADs to be relevant in applied contexts, they must provide insights into species interactions that can inform on community functioning, persistence and change. However, SADs are single observations in time based on species richness and abundance, and thus cannot directly assess interactions, even if their shape (e.g. lognormal vs logseries) suggests the influence of niche-based or stochastic mechanisms. Similar limitations apply when comparing SADs to null expectations (i.e. using null models) or to neutral models (i.e. assuming ecological equivalence). Because the choice of null or neutral models is somewhat arbitrary, any observed deviation does not directly quantify assembly processes (de Bello, 2012). In Box 1, we highlight three key aspects of community assembly: stability (resistance to disturbance), vulnerability (susceptibility to stressors) and functioning, which are connected directly or indirectly with species interactions. We argue that these aspects of community assembly need to be integrated in the study of SADs to make them useful for applied ecology.

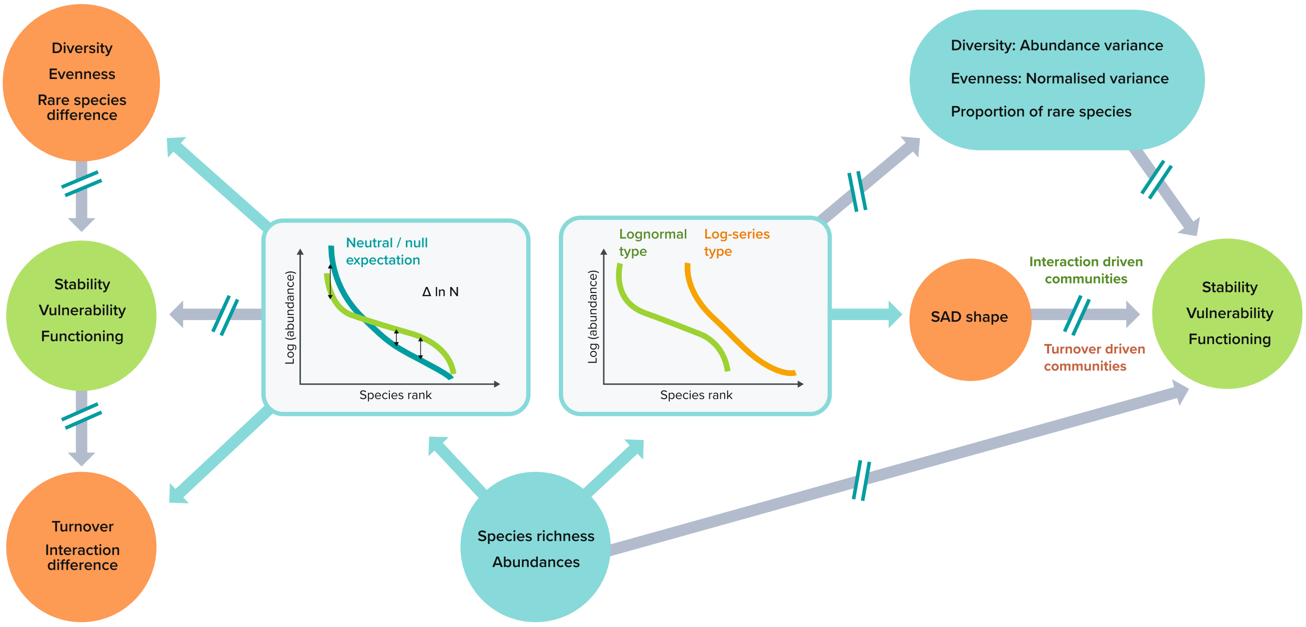
Comparisons of multiple SADs stemming either from temporal or spatial sampling in combination with environmental data might allow for a better understanding of the underlying assembly mechanisms (Box 2). Still, no inference about community functioning is possible due to the lack of information on the ecology of species. The change in species dominance order, diversity or evenness tells

BOX 1 SAD shape and community characteristics

The species abundance distribution (SAD) of a community is generated from species abundances and richness, and these two together fully determine the shape of the SAD (examples here are lognormal and log-series shapes) and a number of derived (condensed) measures related to the abundance distribution, namely the diversity, evenness and proportion of rare species (grey arrows). However, these derived measures can be calculated without generating the full SAD. Strictly, SAD approaches are those that use information about the shape of the entire distribution and of the species rank orders. Richness, abundance and the SAD itself neither quantify species interactions, trait expression nor functioning (indicated by crossed out arrows). Single SADs are point measures and thus do not quantify the temporal or spatial dynamics of communities. Therefore, SADs alone do not directly quantify functioning, stability and vulnerability.

An alternative approach involves comparing the observed SAD to a null or neutral expectation (the left part of the figure) and focusing on the differences between observed and predicted abundances. Again, these differences do not quantify functional attributes, and the null/neutral model choice is to a certain degree arbitrary and artificial. Therefore, this approach also cannot unequivocally quantify functioning, stability and vulnerability.

Single species abundance distributions cannot quantify important community attributes used in ecosystem management and diversity forecasting.



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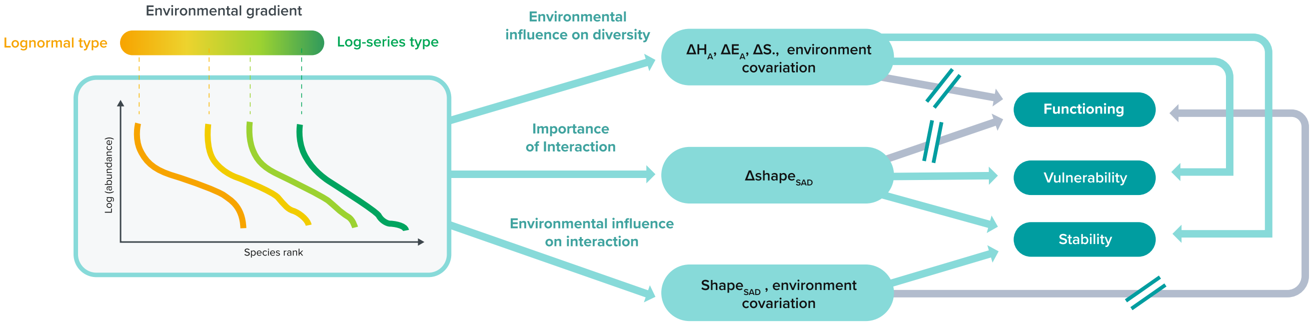
BOX 2 Multiple SADs and community characteristics

The multiple SAD approach uses SAD time series or spatially resolved SADs, ideally in combination with environmental data. Due to the lack of species trait data, no inference about community functioning is possible, even under the additional assumption of a positive diversity–functioning relationship (crossed out arrows). The strength of changes in the SAD might tell about altered community composition, and possibly vulnerability, in dependence on environmental gradients. Changes in dominance order and evenness provide information about compositional community stability.

The use of multiple SADs in combination with environmental data might allow for the assessment of vulnerability and community stability.



us about altered community composition and dominance (Jarzyna et al., 2022; Zhao et al., 2022). The respective strength of change in time or space might provide information about community vulnerability (Hillebrand et al., 2018). Combined with environmental data, this also enables an assessment of compositional stability (Box 2). For example, Jarzyna et al. (2022) reported that temporal variability in species abundances increased, and low richness and evenness decreased; the stability of total community abundance over a wide range of taxa. McCarthy et al. (2018) took the opposite approach and predicted the temporal change of SADs from climate models. As such predictions rely on several basic assumptions about the generation of SADs, further research is necessary to validate them.

4 | FROM SADS TO TADS

Given the above discussion, it is clear that the question of what the study of SADs tells us about ecosystem management, conservation, resource demands or biodiversity forecasting is still open (Figure 1). Integration of functional traits has been suggested as a way forward to better link SADs to community assembly dynamics (Koffel et al., 2022). Functional traits are the phenological and morphological characteristics of a species and express their strategy to persist in a community. Dispersal ability, growth rate, competitive ability or resource use are examples of such traits (Laughlin et al., 2015). The pattern of relative species abundance in combination with species traits influences community functioning (Dee et al., 2019; Lavorel & Garnier, 2002), resource demands (Venier & Fahrig, 1996) and ecosystem services (Dee et al., 2019). Importantly, making inferences about ecological mechanisms from the study of SADs needs information on the distribution of species trait expressions along the dominance rank order (Violle et al., 2007). Interestingly, most work so far has used resource availability to predict species abundances (e.g. Laughlin et al., 2015). Approaching the question from the opposite direction—from abundances to resource availability—and therefore focusing on the use of the SAD as a tool to predict resources and community functioning, is the basis behind many trait-based approaches to functional ecology (Enquist et al., 2019; McGill et al., 2006). These form the basis for extending the concept of the SAD to include species traits.

Distributions of abundance, or traits like biomass, consumption or population growth rates stem from a manifold of ecological processes and interactions and are most often quantified directly at the population level. In contrast, traits like body size, specific leaf area or reproductive output are commonly quantified at the individual level and need to be extrapolated as population or species weighted means. At the species level, we can rank these ecological traits (single traits or respective trait spaces) in a similar way as SADs, the latter then becoming only a special case of a wider concept. The respective trait abundance distribution (TAD) provides information on the distribution of trait expression along the species dominance order (Koffel et al., 2022; Laughlin et al., 2015; cf. Henderson & Magurran, 2010 for alternative approaches). The appropriate combinations of traits would produce a joint TAD representing the order of niche spaces among species. Importantly, TADs of different functional traits could produce different distributions for the same system depending on the ecological strategy each trait confers. This feature might open the door to predict TAD shapes

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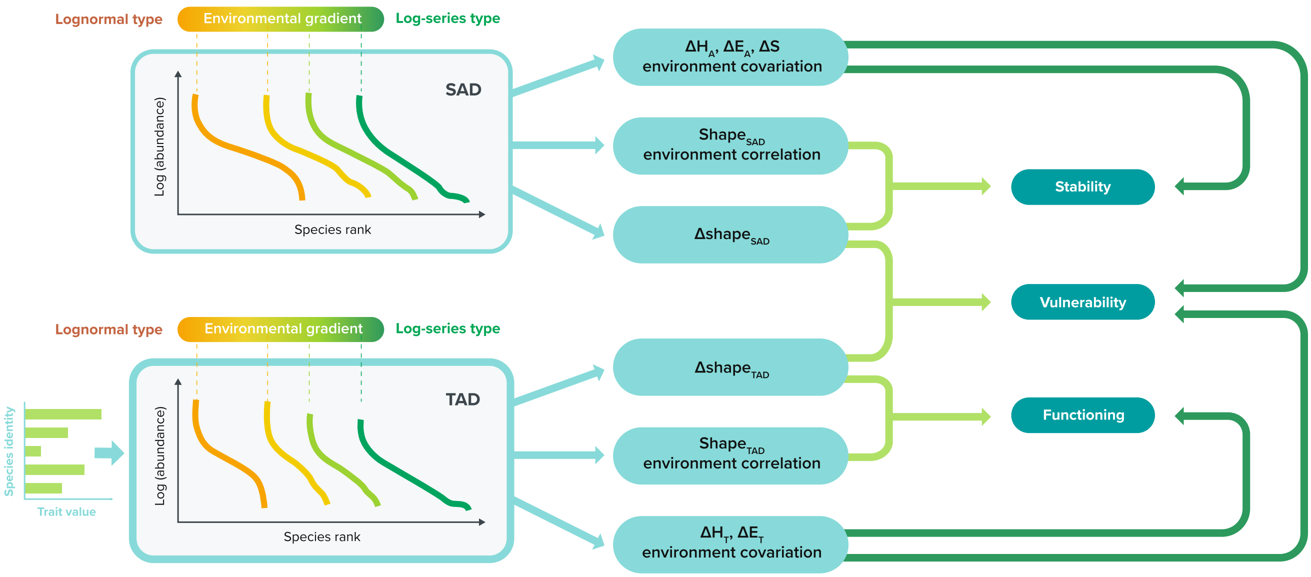
BOX 3 SADs and TADs and community characteristics

Trait-based approaches to SADs combine species abundance and species trait abundance distributions (TAD), the latter being based on species identities and specific trait values. The analysis of changes in SAD and TAD shape and TAD–environment covariability enables the assessment of community stability similar to the multiple SAD approach (Box 2). This approach identifies the most vulnerable species with respect to trait expression. The TAD approach also quantifies changes in community functioning. The use of multiple TADs allows for the comparison of the ranking of species according to their contribution to functional diversity. It indicates which species are most important and which are redundant in a functional context. Changes in these rankings after disturbance provide information about the impact of disturbance on the functional importance of single species. Similar pattern of change in ranking across different communities would indicate general rules of community reassembly after disturbance, being important in an applied context. For example, a tendency towards higher trait ranks of subordinate species after a decline of dominants would corroborate respective insurance models of functional stability and would identify those traits most responsible for this mechanism. Further, the comparison of the abundance and trait ranks of dominant, subordinate and rare species quantifies the degree of functional complementarity of these groups.

An appropriately designed study of trait abundance distributions provides information about community stability, vulnerability and functioning.



after disturbance. For example, if disturbance of a plant community favours the colonisation of wind dispersed species, we might predict a shift in the TADs of some traits (seed size, longevity and plant height).

TADs can be calculated if species-specific trait values are available, preferably coded at a metric scale. Trait relative abundance (t_i) then equals

$$t_i = \frac{n_i c_i}{\sum_{k=1}^{S} n_k c_k}, \tag{1}$$

where n_i and c_i denote the trait value (c) and abundance value of species i, respectively. This is equivalent to the community-weighted mean (CWM) trait value approaches of Garnier et al. (2004) and Violle et al. (2007). The species abundance can be interpreted as a weight factor of trait expression. In the case of the SAD, the specific trait value is 1 for all species (i.e. SADs are a special case of TADs where no trait modifies abundance—each species contributes equally in trait terms).

So far, TADs have gained much less interest than SADs (Koffel et al., 2022; Laughlin et al., 2015; Matthews & Whittaker, 2015), likely due to the lack of appropriate trait data for many taxa. One exception is Pagel et al. (1991), who showed that the biomass distribution in natural communities is generally less even than the associated abundance distribution and that dominant species take much more resources than expected on the basis of their relative abundance (but see Taper & Marquet, 1996). More recent examples include Schrader et al. (2023), who analysed plant species trait data using the framework of island biogeography theory and reported equilibrial trait distributions through time despite high species turnover, and Garbowski et al. (2024), who showed how naturalised alien species can alter the trait distributions of North American plant communities. These previous studies have

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indicated that trait rank order appears to be more stable across plant communities than the respective abundance distributions, making the TAD potentially more sensitive to environmental changes. Here, we argue that, in the context of these previous findings in addition to the increasing availability of trait data for many groups, TADs could have much wider usage in applied ecology in the future. In particular, the comparison of SADs and TADs in combination with environmental data might provide valuable information about community processes, such as niche division and resource states (Box 3). This can be achieved through comparisons of the respective species rank orders, by correlating the parameters of fitted abundance models with environmental data, or by ordination. We note that in the case of abundance data stemming from multiple measurements, the TAD approach might be seen as being complementary to a fourth corner analysis (Legendre et al., 1997) using a trait vector, the abundance matrix and an environmental vector. However, the first step of fourth corner analysis calculates a single community-wide trait value, while TADs retain the trait information for each species.

Functional traits are generally not randomly distributed along the abundance rank order, as each community has its own specific ecological constraints that select for specific trait values (Gross et al., 2021; Li et al., 2021). Indeed, Kazakou et al. (2014) and Mudrák et al. (2019) observed consistent trait rank orders of natural plant communities across plots and spatial scales. In an applied context, changes in species composition, for instance, those induced by disturbance, the introduction of alien species or changes in environmental conditions might change the TAD in a predictable way, although specific TAD models that would predict such changes are still lacking. Specifically, disturbance events may selectively favour traits associated with rapid growth, high dispersal ability or generalist resource use, leading to increased abundances of species possessing these traits. Conversely, traits associated with low dispersal capacity, specialised resource requirements or sensitivity to environmental changes may become less common or disappear entirely. As a result, shifts in the TAD can provide meaningful insights into the nature of the disturbance, its severity and its broader ecological implications, enabling better prediction and management of community-level responses.

5 | EXAMPLE APPLICATIONS OF THE TAD IN APPLIED ECOLOGY

To exemplify the use of TADs in disturbance analysis, we focus on two empirical case studies. First, we reanalyse data from a disturbance experiment in a German beech forest (Ulrich, 1998; raw data in Ulrich, 2023). Ulrich (1998) compared the abundance distributions of soil-associated parasitic Hymenopteran wasps from control plots (i.e. undisturbed plots) with normal leaf cover, and then two categories of disturbed plots: plots where the leaf cover had been removed for 3 years, and plots with fivefold leaf cover for 3 years. Species richness and total wasp densities were highest in the control plots (Figure 4a; Ulrich, 1998). The abundance distributions on all three plot types were best fitted by the log-series distribution, with similar variance (Figure 4a). However, in contrast, TADs built using body dry weight as the focal trait revealed differences between the undisturbed and the disturbed plots. The TAD from the control plots was well fitted by a lognormal distribution, while those from the disturbed plots were still best characterised by the logseries (Figure 4b). Total biomass on the control plots was four times higher than on the litter-free and two times higher than on the fivefold litter plots

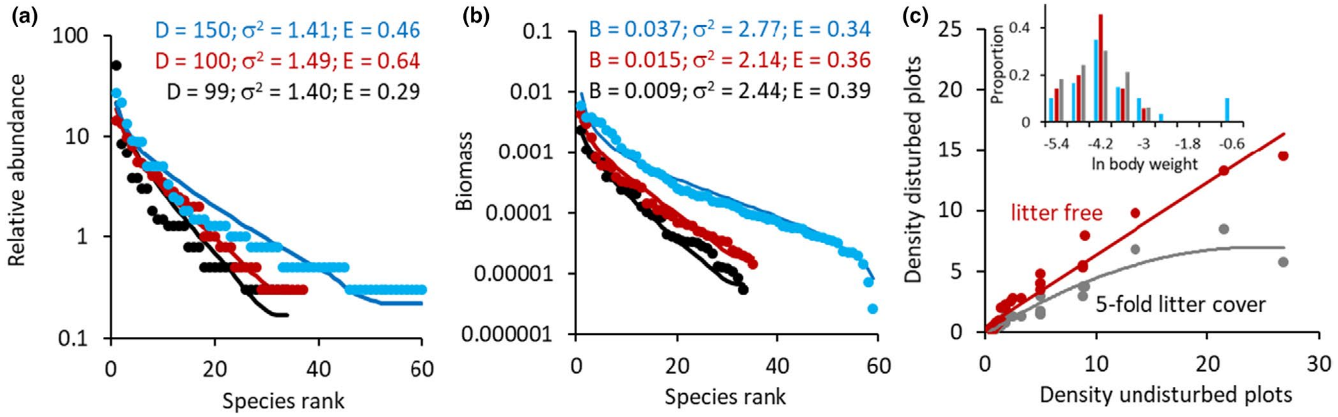

FIGURE 4 SADs (a) and TADs based on species dry weight (b) of parasitic forest Hymenoptera from plots without leaf litter (brown) and fivefold litter layer (black), and undisturbed control plots (blue). The best fit SAD models are shown in each case, which is the logseries for all cases except for the control plots in (b), where a lognormal distribution provided a better fit. D: Total species densities in individuals $\times m^2 \times a^{-1}$. B: Total biomass in mg $\times m^2 \times a^{-1}$, σ^2: Variance of the distributions, and E: Pielou evenness. (c) Species densities (individuals $m^{-2} a^{-1}$) on the litter free (blue dots and best fitting linear regression line, $r^2 = 0.95$) and fivefold litter plots (grey dots and best fitting second order polynomial regression, $r^2 = 0.93$) are positively correlated with those on the undisturbed control plots and the subtle differences in the scaling of abundances caused the differences between the SADs and TADs in (a) and (b). The inlet in (c) (colours as in a and b) shows that the disturbed plots lacked (six) larger wasp species and that the litter free plots had the narrowest size distributions. SAD, species abundance distribution; TAD, trait abundance distribution.

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(Figure 4b; Ulrich, 1998). SAD and TAD species rank orders within and across the control and experimental plots were not significantly correlated (all Spearman rank order correlations $r_S < 0.34$, $p > 0.1$) indicating the reshuffling of species ranks from SADs to TADs and further highlighting the importance of using trait data to assess the functional importance of individual species in analyses of this nature. Comparisons of densities and body sizes between plots (Figure 4c) indicate that these differences were caused by subtle variation in the scaling of abundances between plots and by filter effects for body size. Disturbed plots lacked larger species, and litter-free plots in particular had relatively narrow body size distributions. The use of TADs enabled these differences to become statistically detectable while also accounting for changes in species abundance (e.g. some larger species becoming rarer but still persisting in low numbers), which are obscured when focusing on species-level metrics only (e.g. standard body-size distributions). Figure 4 also demonstrates that the use of evenness metrics might be misleading in community comparisons as the values are distributed counterintuitively across the SADs while being very similar for the three TADs.

As a second example, Ulrich et al. (2024) compared the TADs and SADs of European grassland plant communities as well as changes in dominance classes to assess the importance of different environmental drivers. Their analyses found climate seasonality to be an important factor influencing SAD and TAD shape as well as differences in the proportional abundances of subordinate species and community evenness. Contrary to the wasp example above, SAD and TAD rank orders were positively correlated. Neutral processes, which assume species trait equivalence, should effectively randomise the species rank orders of the TAD with respect to the SAD. The observed positive co-variation of SAD and TAD plant ranks therefore rejects such a pure stochastic model of community assembly. However, more work, particularly on animals, is necessary to extract the mechanisms necessary for a precise assessment of expected TAD shapes in various taxa. Importantly, traits should be chosen a priori based on precise assumptions about their functional value and possible reactions to disturbances. The expansion of the TAD to multidimensional functional diversity is also an interesting future research direction.

6 | CONCLUSIONS

The review and the literature survey did not point to straightforward applications of SADs and unequivocal interpretation of SAD patterns in an applied ecological context. The major restriction is the fact that different ecological processes can generate similar dominance distributions and therefore SADs. In particular, SADs alone do not quantify the amount or specific impacts of disturbance and only provide limited insight into ecosystem functioning. However, SADs may still be useful applied tools if used in combination with environmental data and with information on species identity and functional traits.

We argue that SADs are a special case of a wider concept: the trait abundance distribution. Only the comparison of different TADs might allow for an assessment of mechanisms that influence community assembly and (abundance based) dominance orders. However, to be fully informative in an applied context, comparisons of this nature arguably need to be accompanied by environmental data or data on species interactions. Currently, the TAD of individual traits cannot be predicted from observed abundance distributions alone. Trait selection might heavily influence the SAD–TAD relationship, but we only start to understand the mechanisms behind this relationship that would allow us to predict trait specific TADs, for instance, body size and biomass from metabolic theory (Allen et al., 2002). We thus call for the development of a theoretical approach to understand the links between trait expression and abundance under different environmental conditions. Metabolic and quasi-neutral approaches that include species traits might be useful in developing such a theory (e.g. Jabot et al., 2008; Schramski et al., 2015).

AUTHOR CONTRIBUTIONS

Our study was a global review and was based on a meta-analysis of secondary data rather than primary data. As such, there was no local data collection. Werner Ulrich conceived the study, analysed data and wrote the first draft. Paulo Borges and Simone Fattorini contributed datasets and analysed data. Pablo Marquet improved the Figures. Anne Magurran, Julian Schrader, Tom Mathews, Hans ter Steege and Nicholas Gotelli wrote part of the text. All authors revised and contributed to the final text version.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

As this is a review, references of publications used for the literature survey are contained in Appendix S1.

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REFERENCES

Allen, A. P., Brown, J. H., & Gillooly, J. F. (2002). Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, *297*, 1545–1548. https://doi.org/10.1126/science.1072380

Allesina, S., & Tang, S. (2012). Stability criteria for complex ecosystems. *Nature*, *483*, 205–208. https://doi.org/10.1038/nature10832

Alroy, J. (2015). The shape of terrestrial abundance distributions. *Science Advances*, *1*, e1500082. https://doi.org/10.1126/sciadv.1500082

Antão, L. H., Magurran, A. E., & Dornelas, M. (2021). The shape of species abundance distributions across spatial scales. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.626730

Autio, O., Salmela, J., & Suhonen, J. (2013). Species richness and rarity of crane flies (Diptera, Tipuloidea) in a boreal mire. *Journal of Insect Conservation*, *17*, 1125–1136. https://doi.org/10.1007/s10841-013-9593-5

Baldridge, E., Harris, D. J., Xiao, X., & White, E. P. (2016). An extensive comparison of species-abundance distribution models. *PeerJ*, *4*, e2823. https://doi.org/10.7717/peerj.2823

Barrett, I. C., McIntosh, A. R., & Warburton, H. J. (2023). Community type and disturbance type interact to determine disturbance response: Implications for extending the environmental filter metaphor. *Community Ecology*, *24*, 257–269. https://doi.org/10.1007/s42974-023-00149-3

Borda-de-Água, L. (2019). The importance of scaling in biodiversity. In E. Casetta, J. Marques da Silva, & D. Vecchi (Eds.), *From assessing to conserving biodiversity: Conceptual and practical challenges* (pp. 107–122). Springer International Publishing. https://doi.org/10.1007/978-3-030-10991-2_5

Bowler, M. G. (2014). Species abundance distributions, statistical mechanics and the priors of MaxEnt. *Theoretical Population Biology*, *92*, 69–77. https://doi.org/10.1016/j.tpb.2013.12.002

Brush, M., & Harte, J. (2021). Relating the strength of density dependence and the spatial distribution of individuals. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.691792

Brush, M., Matthews, T. J., Borges, P. A. V., & Harte, J. (2022). Land use change through the lens of macroecology: Insights from Azorean arthropods and the maximum entropy theory of ecology. *Ecography*, *2022*, e06141. https://doi.org/10.1111/ecog.06141

de Bello, F. (2012). The quest for trait convergence and divergence in community assembly: Are null-models the magic wand? *Global Ecology and Biogeography*, *21*, 312–317. https://doi.org/10.1111/j.1466-8238.2011.00682.x

de Lima, R. A. F., Condé, P. A., Banks-Leite, C., Campos, R. C., Hernández, M. I. M., Rodrigues, R. R., & Prado, P. I. (2020). Disentangling the effects of sampling scale and size on the shape of species abundance distributions. *PLoS One*, *15*, e0238854. https://doi.org/10.1371/journal.pone.0238854

Dee, L. E., Cowles, J., Isbell, F., Pau, S., Gaines, S. D., & Reich, P. B. (2019). When do ecosystem services depend on rare species? *Trends in Ecology & Evolution*, *34*, 746–758. https://doi.org/10.1016/j.tree.2019.03.010

Diaz, R. M., Ye, H., & Ernest, S. K. M. (2021). Empirical abundance distributions are more uneven than expected given their statistical baseline. *Ecology Letters*, *24*, 2025–2039. https://doi.org/10.1111/ele.13820

Dornelas, M. (2010). Disturbance and change in biodiversity. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *365*, 3719–3727. https://doi.org/10.1098/rstb.2010.0295

Dornelas, M., Moonen, A. C., Magurran, A. E., & Bàrberi, P. (2009). Species abundance distributions reveal environmental heterogeneity in modified landscapes. *Journal of Applied Ecology*, *46*, 666–672. https://doi.org/10.1111/j.1365-2664.2009.01640.x

Engen, S., & Lande, R. (1996). Population dynamic models generating species abundance distributions of the gamma type. *Journal of Theoretical Biology*, *178*, 325–331. https://doi.org/10.1006/jtbi.1996.0028

Enquist, B. J., Feng, X., Boyle, B., Maitner, B., Newman, E. A., Jørgensen, P. M., Roehrdanz, P. R., Thiers, B. M., Burger, J. R., Corlett, R. T., Couvreur, T. L. P., Dauby, G., Donoghue, J. C., Foden, W., Lovett, J. C., Marquet, P. A., Merow, C., Midgley, G., Morueta-Holme, N., … McGill, B. J. (2019). The commonness of rarity: Global and future distribution of rarity across land plants. *Science Advances*, *5*, eaaz0414. https://doi.org/10.1126/sciadv.aaz0414

Etienne, R. S., & Olff, H. (2005). Confronting different models of community structure to species-abundance data: A Bayesian model comparison. *Ecology Letters*, *8*, 493–504. https://doi.org/10.1111/j.1461-0248.2005.00745.x

Fagan, W. F., & Kareiva, P. M. (1997). Using compiled species lists to make biodiversity comparisons among regions: A test case using Oregon butterflies. *Biological Conservation*, *80*, 249–259. https://doi.org/10.1016/S0006-3207(96)00144-9

Fargione, J., Brown, C. S., & Tilman, D. (2003). Community assembly and invasion: An experimental test of neutral versus niche processes. *Proceedings of the National Academy of Sciences of the United States of America*, *100*, 8916–8920. https://doi.org/10.1073/pnas.1033107100

Fattorini, S., Rigal, F., Cardoso, P., & Borges, P. A. V. (2016). Using species abundance distribution models and diversity indices for biogeographical analyses. *Acta Oecologica*, *70*, 21–28. https://doi.org/10.1016/j.actao.2015.11.003

Fisher, C. K., & Mehta, P. (2014). The transition between the niche and neutral regimes in ecology. *Proceedings of the National Academy of Sciences of the United States of America*, *111*, 13111–13116. https://doi.org/10.1073/pnas.1405637111

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. https://doi.org/10.2307/1411

Fraaije, R. G. A., ter Braak, C. J. F., Verduyn, B., Verhoeven, J. T. A., & Soons, M. B. (2015). Dispersal versus environmental filtering in a dynamic system: Drivers of vegetation patterns and diversity along stream riparian gradients. *Journal of Ecology*, *103*, 1634–1646. https://doi.org/10.1111/1365-2745.12460

Garbowski, M., Laughlin, D. C., Blumenthal, D. M., Sofaer, H. R., Barnett, D. T., Beaury, E. M., Buonaiuto, D. M., Corbin, J. D., Dukes, J. S., Early, R., Nebhut, A. N., Petri, L., Vilà, M., & Pearse, I. S. (2024). Naturalized species drive functional trait shifts in plant communities. *Proceedings of the National Academy of Sciences of the United States of America*, *121*, e2403120121. https://doi.org/10.1073/pnas.2403120121

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., & Toussaint, J.-P. (2004). Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, *85*, 2630–2637. https://doi.org/10.1890/03-0799

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. https://doi.org/10.1016/0025-326X(79)90082-1

Gray, J. S., Waldichuck, M., Newton, A. J., Berry, R. J., Holden, A. V., Pearson, T. H., & Cole, H. A. (1997). Pollution-induced changes

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in populations. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *286*, 545–561. https://doi.org/10.1098/rstb.1979.0045

Green, J. L., & Plotkin, J. B. (2007). A statistical theory for sampling species abundances. *Ecology Letters*, *10*, 1037–1045. https://doi.org/10.1111/j.1461-0248.2007.01101.x

Gross, N., Le Bagousse-Pinguet, Y., Liancourt, P., Saiz, H., Violle, C., & Munoz, F. (2021). Unveiling ecological assembly rules from commonalities in trait distributions. *Ecology Letters*, *24*, 1668–1680. https://doi.org/10.1111/ele.13789

Hågvar, S. (1994). Log-normal distribution of dominance as an indicator of stressed soil microarthropod communities? *Acta Zoologica Fennica*, *195*, 71–80.

Hammal, O. A., Alonso, D., Etienne, R. S., & Cornell, S. J. (2015). When can species abundance data reveal non-neutrality? *PLoS Computational Biology*, *11*, e1004134. https://doi.org/10.1371/journal.pcbi.1004134

Hanski, I. (1982). Dynamics of regional distribution: The core and satellite species hypothesis. *Oikos*, *38*, 210–221. https://doi.org/10.2307/3544021

Harte, J. (2011). The maximum entropy theory of ecology (METE). In J. Harte (Ed.), *Maximum entropy and ecology: A theory of abundance, distribution, and energetics*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780199593415.003.0007

Harte, J., Umemura, K., & Brush, M. (2021). DynaMETE: A hybrid MaxEnt-plus-mechanism theory of dynamic macroecology. *Ecology Letters*, *24*, 935–949. https://doi.org/10.1111/ele.13714

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. https://doi.org/10.1098/rspb.2009.2189

Hill, J. K., & Hamer, K. C. (1998). Using species abundance models as indicators of habitat disturbance in tropical forests. *Journal of Applied Ecology*, *35*, 458–460. https://doi.org/10.1046/j.1365-2664.1998.00310.x

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., Van de Waal, D. B., & Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, *55*, 169–184. https://doi.org/10.1111/1365-2664.12959

Hooper, D. U., Chapin, F. S., III, Ewel, J. J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J. H., Lodge, D. M., Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A. J., Vandermeer, J., & Wardle, D. A. (2005). Effects of biodiversity on ecosystem functioning: A consensus of current knowledge. *Ecological Monographs*, *75*, 3–35. https://doi.org/10.1890/04-0922

Horváth, Z., Ptacnik, R., Vad, C. F., & Chase, J. M. (2019). Habitat loss over six decades accelerates regional and local biodiversity loss via changing landscape connectance. *Ecology Letters*, *22*, 1019–1027. https://doi.org/10.1111/ele.13260

Hubbell, S. P. (2001). *The unified neutral theory of biodiversity and biogeography*. Princeton University Press.

Hubbell, S. P., He, F., Condit, R., Borda-de-Água, L., Kellner, J., & ter Steege, H. (2008). How many tree species are there in the Amazon and how many of them will go extinct? *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 11498–11504. https://doi.org/10.1073/pnas.0801915105

Ibanez, T., Keppel, G., Baider, C., Birkinshaw, C., Florens, F. B. V., Laidlaw, M., Menkes, C., Parthasarathy, N., Rajkumar, M., Ratovoson, F., Rasingam, L., Reza, L., Aiba, S., Webb, E. L., Zang, R., & Birnbaum, P. (2020). Tropical cyclones and Island area shape species abundance distributions of local tree communities. *Oikos*, *129*, 1856–1866. https://doi.org/10.1111/oik.07501

Izsák, J. (2005). A pilot study on the frequency structure of histological neoplasm diagnoses in rats. *Journal of Theoretical Biology*, *236*, 427–437. https://doi.org/10.1016/j.jtbi.2005.03.024

Jabot, F., & Chave, J. (2011). Analyzing tropical Forest tree species abundance distributions using a nonneutral model and through approximate Bayesian inference. *The American Naturalist*, *178*, E37–E47. https://doi.org/10.1086/660829

Jabot, F., Etienne, R. S., & Chave, J. (2008). Reconciling neutral community models and environmental filtering: Theory and an empirical test. *Oikos*, *117*, 1308–1320. https://doi.org/10.1111/j.0030-1299.2008.16724.x

Jarzyna, M. A., Norman, K. E. A., LaMontagne, J. M., Helmus, M. R., Li, D., Parker, S. M., Perez Rocha, M., Record, S., Sokol, E. R., Zarnetske, P. L., & Surasinghe, T. D. (2022). Community stability is related to animal diversity change. *Ecosphere*, *13*, e3970. https://doi.org/10.1002/ecs2.3970

Kazakou, E., Violle, C., Roumet, C., Navas, M.-L., Vile, D., Kattge, J., & Garnier, E. (2014). Are trait-based species rankings consistent across data sets and spatial scales? *Journal of Vegetation Science*, *25*, 235–247. https://doi.org/10.1111/jvs.12066

Keen, K. A., Beltran, R. S., Pirotta, E., & Costa, D. P. (2021). Emerging themes in population consequences of disturbance models. *Proceedings of the Royal Society B: Biological Sciences*, *288*, 20210325. https://doi.org/10.1098/rspb.2021.0325

Kim, D. W., 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. https://doi.org/10.1016/j.ecoinf.2013.06.006

Kitzes, J., & Harte, J. (2015). Predicting Extinction Debt from Community Patterns. *Ecology*, *96*, 2127–2136. https://doi.org/10.1890/14-1594.1

Koffel, T., Umemura, K., Litchman, E., & Klausmeier, C. A. (2022). A general framework for species-abundance distributions: Linking traits and dispersal to explain commonness and rarity. *Ecology Letters*, *25*, 2359–2371. https://doi.org/10.1111/ele.14094

Laughlin, D. C., Joshi, C., Richardson, S. J., Peltzer, D. A., Mason, N. W. H., & Wardle, D. A. (2015). Quantifying multimodal trait distributions improves trait-based predictions of species abundances and functional diversity. *Journal of Vegetation Science*, *26*, 46–57. https://doi.org/10.1111/jvs.12219

Lavorel, S., & Garnier, E. (2002). Predicting changes in community composition and ecosystem functioning from plant traits: Revisiting the holy grail. *Functional Ecology*, *16*, 545–556. https://doi.org/10.1046/j.1365-2435.2002.00664.x

Legendre, P., Galzin, R., & Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: Solutions to Thefourth-corner problem. *Ecology*, *78*, 547–562. https://doi.org/10.1890/0012-9658(1997)078[0547:RBTHST]2.0.CO;2

Li, R., Zhu, S., Lian, J., Zhang, H., Liu, H., Ye, W., & Ye, Q. (2021). Functional traits are good predictors of tree species abundance across 101 subtropical Forest species in China. *Frontiers in Plant Science*, *12*. https://doi.org/10.3389/fpls.2021.541577

Lin, D., Jiang, Y., Zang, R., Wang, X., Long, W., Huang, J., Kang, Y., Wang, X., & Xie, Z. (2016). Patterns of species diversity are not consistent between shifting cultivation in Bawangling Nature Reserves and selective logging in Diaoluoshan Nature Reserves, Hainan Island, China. *Tropical Conservation Science*, *9*, 584–606. https://doi.org/10.1177/194008291600900203

Locey, K. J., & White, E. P. (2013). How species richness and total abundance constrain the distribution of abundance. *Ecology Letters*, *16*, 1177–1185. https://doi.org/10.1111/ele.12154

Magurran, A. E. (2013). *Measuring biological diversity*. Wiley-Blackwell.

Magurran, A. E., & Henderson, P. A. (2003). Explaining the excess of rare species in natural species abundance distributions. *Nature*, *422*, 714–716. https://doi.org/10.1038/nature01547

13652664, 2025, 9, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70140 by Universidade Dos Acores, Wiley Online Library on [22/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

Marquet, P. A., Allen, A. P., Brown, J. H., Dunne, J. A., Enquist, B. J., Gillooly, J. F., Gowaty, P. A., Green, J. L., Harte, J., Hubbell, S. P., O'Dwyer, J., Okie, J. G., Ostling, A., Ritchie, M., Storch, D., & West, G. B. (2014). On theory in ecology. *BioScience*, *64*, 701–710. https://doi.org/10.1093/biosci/biu098

Marquet, P. A., Espinoza, G., Abades, S. R., Ganz, A., & Rebolledo, R. (2017). On the Proportional Abundance of Species: Integrating Population Genetics and Community Ecology. *Scientific Reports*, *7*, 16815. https://doi.org/10.1038/s41598-017-17070-1

Mason, N. W. H., Lanoiselée, C., Mouillot, D., Wilson, J. B., & Argillier, C. (2008). Does niche overlap control relative abundance in French lacustrine fish communities? A new method incorporating functional traits. *Journal of Animal Ecology*, *77*, 661–669. https://doi.org/10.1111/j.1365-2656.2008.01379.x

Matthews, T. J. (2021). On the biogeography of Habitat Islands: The importance of matrix effects, noncore species, and source-sink dynamics. *The Quarterly Review of Biology*, *96*, 73–104. https://doi.org/10.1086/714482

Matthews, T. J., Borges, P. A. V., de Azevedo, E. B., & Whittaker, R. J. (2017). A biogeographical perspective on species abundance distributions: Recent advances and opportunities for future research. *Journal of Biogeography*, *44*, 1705–1710. https://doi.org/10.1111/jbi.13008

Matthews, T. J., Sadler, J. P., Kubota, Y., Woodall, C. W., & Pugh, T. A. M. (2019). Systematic variation in North American tree species abundance distributions along macroecological climatic gradients. *Global Ecology and Biogeography*, *28*, 601–611. https://doi.org/10.1111/geb.12879

Matthews, T. J., & Whittaker, R. J. (2014). Neutral theory and the species abundance distribution: Recent developments and prospects for unifying niche and neutral perspectives. *Ecology and Evolution*, *4*, 2263–2277. https://doi.org/10.1002/ece3.1092

Matthews, T. J., & Whittaker, R. J. (2015). REVIEW: On the species abundance distribution in applied ecology and biodiversity management. *Journal of Applied Ecology*, *52*, 443–454. https://doi.org/10.1111/1365-2664.12380

May, R. (1975). Patterns of species abundance and diversity. In *Ecology and evolution of communities* (pp. 81–120). Harvard University Press.

McCarthy, J. K., Mokany, K., Ferrier, S., & Dwyer, J. M. (2018). Predicting community rank-abundance distributions under current and future climates. *Ecography*, *41*, 1572–1582. https://doi.org/10.1111/ecog.03552

McGill, B. J. (2010). Towards a unification of unified theories of biodiversity. *Ecology Letters*, *13*, 627–642. https://doi.org/10.1111/j.1461-0248.2010.01449.x

McGill, B. J., Enquist, B. J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, *21*, 178–185. https://doi.org/10.1016/j.tree.2006.02.002

McGill, B. J., Etienne, R. S., Gray, J. S., Alonso, D., Anderson, M. J., Benecha, H. K., Dornelas, M., Enquist, B. J., Green, J. L., He, F., Hurlbert, A. H., Magurran, A. E., Marquet, P. A., Maurer, B. A., Ostling, A., Soykan, C. U., Ugland, K. I., & White, E. P. (2007). Species abundance distributions: Moving beyond single prediction theories to integration within an ecological framework. *Ecology Letters*, *10*, 995–1015. https://doi.org/10.1111/j.1461-0248.2007.01094.x

McMullen, L. E., De Leenheer, P., Tonkin, J. D., & Lytle, D. A. (2017). High mortality and enhanced recovery: Modelling the countervailing effects of disturbance on population dynamics. *Ecology Letters*, *20*, 1566–1575. https://doi.org/10.1111/ele.12866

Moradi, H., Prado, P. I., Oldeland, J., Borges, P. A. V., & Fattorini, S. (2025). Use of cover data to model species abundance distributions through continuous probability functions. *Scientific Reports*, *15*, 11361. https://doi.org/10.1038/s41598-025-94587-w

Morlon, H., White, E. P., Etienne, R. S., Green, J. L., Ostling, A., Alonso, D., Enquist, B. J., He, F., Hurlbert, A., Magurran, A. E., Maurer, B. A., McGill, B. J., Olff, H., Storch, D., & Zillio, T. (2009). Taking species abundance distributions beyond individuals. *Ecology Letters*, *12*, 488–501. https://doi.org/10.1111/j.1461-0248.2009.01318.x

Motomura, I. (1932). On the statistical treatment of communities. *Zoological Magazine*, *44*, 379–383. x.

Mudrák, O., Doležal, J., Vítová, A., & Lepš, J. (2019). Variation in plant functional traits is best explained by the species identity: Stability of trait-based species ranking across meadow management regimes. *Functional Ecology*, *33*, 746–755. https://doi.org/10.1111/1365-2435.13287

Myers, J. A., & Harms, K. E. (2009). Seed arrival, ecological filters, and plant species richness: A meta-analysis. *Ecology Letters*, *12*, 1250–1260. https://doi.org/10.1111/j.1461-0248.2009.01373.x

Nemergut, D. R., Schmidt, S. K., Fukami, T., O'Neill, S. P., Bilinski, T. M., Stanish, L. F., Knelman, J. E., Darcy, J. L., Lynch, R. C., Wickey, P., & Ferrenberg, S. (2013). Patterns and processes of microbial community assembly. *Microbiology and Molecular Biology Reviews*, *77*, 342–356. https://doi.org/10.1128/mmbr.00051-12

Newman, E. A., Wilber, M. Q., Kopper, K. E., Moritz, M. A., Falk, D. A., McKenzie, D., & Harte, J. (2020). Disturbance macroecology: A comparative study of community structure metrics in a high-severity disturbance regime. *Ecosphere*, *11*, e03022. https://doi.org/10.1002/ecs2.3022

O'Grady, J. J., Reed, D. H., Brook, B. W., & Frankham, R. (2004). What are the best correlates of predicted extinction risk? *Biological Conservation*, *118*, 513–520. https://doi.org/10.1016/j.biocon.2003.10.002

Pagel, M. D., Harvey, P. H., & Godfray, H. C. J. (1991). Species-abundance, biomass, and resource-use distributions. *The American Naturalist*, *138*, 836–850. https://doi.org/10.1086/285255

Preston, F. W. (1948). The commonness, and rarity, of species. *Ecology*, *29*, 254–283. https://doi.org/10.2307/1930989

Preston, F. W. (1980). Noncanonical distributions of commonness and rarity. *Ecology*, *61*, 88–97. https://doi.org/10.2307/1937159

Remadevi, O. K., Manjunatha, M., Sharma, B., Saritha, B., Poorvashree, P., Suresh, H. S., Kumar, K. H. V., Kakkar, R., Singh, R. K., & Gadow, K. V. (2023). Analysing highly biodiverse tropical dry forests for improved conservation. *European Journal of Forest Research*, *142*, 641–656. https://doi.org/10.1007/s10342-023-01547-y

Riffo-Donoso, V., Osorio, F., & Fontúrbel, F. E. (2021). Habitat disturbance alters species richness, composition, and turnover of the bryophyte community in a temperate rainforest. *Forest Ecology and Management*, *496*, 119467. https://doi.org/10.1016/j.foreco.2021.119467

Schrader, J., Wright, I. J., Kreft, H., Weigelt, P., Andrew, S. C., Abbott, I., & Westoby, M. (2023). ETIB-T: An equilibrium theory of Island biogeography for plant traits. *Journal of Biogeography*, *50*, 223–234. https://doi.org/10.1111/jbi.14526

Schramski, J. R., Dell, A. I., Grady, J. M., Sibly, R. M., & Brown, J. H. (2015). Metabolic theory predicts whole-ecosystem properties. *Proceedings of the National Academy of Sciences of the United States of America*, *112*, 2617–2622. https://doi.org/10.1073/pnas.1423502112

Shipley, B., Vile, D., & Garnier, É. (2006). From plant traits to plant communities: A statistical mechanistic approach to biodiversity. *Science*, *314*, 812–814. https://doi.org/10.1126/science.1131344

Smith, E. A., Holden, E. M., Brown, C., & Jr, J. F. C. (2022). Disturbance has lasting effects on functional traits and diversity of grassland plant communities. *PeerJ*, *10*, e13179. https://doi.org/10.7717/peerj.13179

Smith, K. G., & Almeida, R. J. (2020). When are extinctions simply bad luck? Rarefaction as a framework for disentangling selective and stochastic extinctions. *Journal of Applied Ecology*, *57*, 101–110. https://doi.org/10.1111/1365-2664.13510

Solbu, E. B., van der Veen, B., Herfindal, I., & Hovstad, K. A. (2022). Analyzing dynamic species abundance distributions using

13652664, 2025, 9, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70140 by Universidade Dos Acores, Wiley Online Library on [22/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License

generalized linear mixed models. *Ecology*, *103*, e3742. https://doi.org/10.1002/ecy.3742

Taper, M. L., & Marquet, P. A. (1996). How do species really divide resources? *The American Naturalist*, *147*, 1072–1086. https://doi.org/10.1086/285893

ter Steege, H., Pitman, N. C. A., Sabatier, D., Baraloto, C., Salomão, R. P., Guevara, J. E., Phillips, O. L., Castilho, C. V., Magnusson, W. E., Molino, J.-F., Monteagudo, A., Núñez Vargas, P., Montero, J. C., Feldpausch, T. R., Coronado, E. N. H., Killeen, T. J., Mostacedo, B., Vasquez, R., Assis, R. L., … Silman, M. R. (2013). Hyperdominance in the Amazonian tree flora. *Science*, *342*, 1243092. https://doi.org/10.1126/science.1243092

ter Steege, H., Prado, P. I., de Lima, R. A. F., Pos, E., de Souza Coelho, L., Andrade, d., Lima Filho, D., Salomão, R. P., Amaral, I. L., de Almeida Matos, F. D., Castilho, C. V., Phillips, O. L., Guevara, J. E., de Jesus Veiga Carim, M., Cárdenas López, D., Magnusson, W. E., Wittmann, F., Martins, M. P., Sabatier, D., … Pickavance, G. (2020). Biased-corrected richness estimates for the Amazonian tree flora. *Scientific Reports*, *10*, 10130. https://doi.org/10.1038/s41598-020-66686-3

Terra, M. d. C. N. S., dos Santos, R. M., Fontes, M. A. L., de Mello, J. M., Scolforo, J. R. S., Gomide, L. R., do Prado Júnior, J. A., Schiavini, I., & ter Steege, H. (2017). Tree dominance and diversity in Minas Gerais, Brazil. *Biodiversity and Conservation*, *26*, 2133–2153. https://doi.org/10.1007/s10531-017-1349-1

Tokeshi, M. (2009). *Species coexistence: Ecological and evolutionary perspectives*. Wiley-Blackwell.

Trubovitz, S., Renaudie, J., Lazarus, D., & Noble, P. J. (2023). Abundance does not predict extinction risk in the fossil record of marine plankton. *Communications Biology*, *6*, 1–10. https://doi.org/10.1038/s42003-023-04871-6

Turnbull, L. A., Isbell, F., Purves, D. W., Loreau, M., & Hector, A. (2016). Understanding the value of plant diversity for ecosystem functioning through niche theory. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20160536. https://doi.org/10.1098/rspb.2016.0536

Ugland, K. I., & Gray, J. S. (1982). Lognormal distributions and the concept of community equilibrium. *Oikos*, *39*, 171–178. https://doi.org/10.2307/3544482

Ulrich, W. (1998). The parasitic hymenoptera in a beech forest on limestone III: The role of leaf litter for the parasitod species. *Polish Journal of Ecology*, *46*, 311–326.

Ulrich, W. (2023). Hymenoptera of a German beech forest. *figshare*, https://doi.org/10.6084/m9.figshare.22188571

Ulrich, W., Jabot, F., & Gotelli, N. J. (2017). Competitive interactions change the pattern of species co-occurrences under neutral dispersal. *Oikos*, *126*, 91–100. https://doi.org/10.1111/oik.03392

Ulrich, W., Matthews, T. J., Biurrun, I., Aleksanyan, A., Borovyk, D., Burrascano, S., Campos, J. A., Chusova, O., Czarniecka-Wiera, M., Czortek, P., Dembicz, I., Essl, F., Janišová, M., Labadessa, R., Napoleone, F., Pielech, R., Vynokurov, D., & Puchałka, R. (2024). *The proper middle class: Assessing the importance of species with intermediate abundance on plant community assembly and functional diversity*. Elsevier BV. https://doi.org/10.2139/ssrn.5057267

Ulrich, W., Matthews, T. J., Biurrun, I., Campos, J. A., Czortek, P., Dembicz, I., Essl, F., Filibeck, G., del Galdo, G.-P. G., Güler, B., Naqinezhad, A., Török, P., & Dengler, J. (2022). Environmental drivers and spatial scaling of species abundance distributions in Palaearctic grassland vegetation. *Ecology*, *103*, e3725. https://doi.org/10.1002/ecy.3725

Ulrich, W., Matthews, T. J., & Kubota, Y. (2020). Constraints on the distribution of species abundances indicate universal mechanisms of community assembly. *Ecological Research*, *35*, 362–371. https://doi.org/10.1111/1440-1703.12095

Ulrich, W., Nakadai, R., Matthews, T. J., & Kubota, Y. (2018). The two-parameter Weibull distribution as a universal tool to model the variation in species relative abundances. *Ecological Complexity*, *36*, 110–116. https://doi.org/10.1016/j.ecocom.2018.07.002

Ulrich, W., & Ollik, M. (2005). Limits to the estimation of species richness: The use of relative abundance distributions. *Diversity and Distributions*, *11*, 265–273. https://doi.org/10.1111/j.1366-9516.2005.00127.x

Ulrich, W., Ollik, M., & Ugland, K. I. (2010). A meta-analysis of species-abundance distributions. *Oikos*, *119*, 1149–1155. https://doi.org/10.1111/j.1600-0706.2009.18236.x

Ulrich, W., Soliveres, S., Thomas, A. D., Dougill, A. J., & Maestre, F. T. (2016). Environmental correlates of species rank - abundance distributions in global drylands. *Perspectives in Plant Ecology, Evolution and Systematics*, *20*, 56–64. https://doi.org/10.1016/j.ppees.2016.04.004

Venier, L. A., & Fahrig, L. (1996). Habitat availability causes the species abundance–distribution relationship. *Oikos*, *76*, 564–570. https://doi.org/10.2307/3546349

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, *116*, 882–892. https://doi.org/10.1111/j.0030-1299.2007.15559.x

Warton, D. I., Shipley, B., & Hastie, T. (2015). CATS regression—A model-based approach to studying trait-based community assembly. *Methods in Ecology and Evolution*, *6*, 389–398. https://doi.org/10.1111/2041-210X.12280

Whittaker, R. H. (1965). Dominance and diversity in land plant communities. *Science*, *147*, 250–260. https://doi.org/10.1126/science.147.3655.250

Yen, J. D. L., Thomson, J. R., & Mac Nally, R. (2013). Is there an ecological basis for species abundance distributions? *Oecologia*, *171*, 517–525. https://doi.org/10.1007/s00442-012-2438-1

Zhao, L., Wang, S., Shen, R., Gong, Y., Wang, C., Hong, P., & Reuman, D. C. (2022). Biodiversity stabilizes plant communities through statistical-averaging effects rather than compensatory dynamics. *Nature Communications*, *13*, 7804. https://doi.org/10.1038/s41467-022-35514-9

Zhou, S.-R., & Zhang, D.-Y. (2008). A nearly neutral model of biodiversity. *Ecology*, *89*, 248–258. https://doi.org/10.1890/06-1817.1

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Literature survey.

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13652664, 2025, 9, Downloaded from https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2664.70140 by Universidade Dos Acores, Wiley Online Library on [22/01/2026]. See the Terms and Conditions (https://onlinelibrary.wiley.com/terms-and-conditions) on Wiley Online Library for rules of use; OA articles are governed by the applicable Creative Commons License