Disentangling components of diversity scaling along biogeographic gradients

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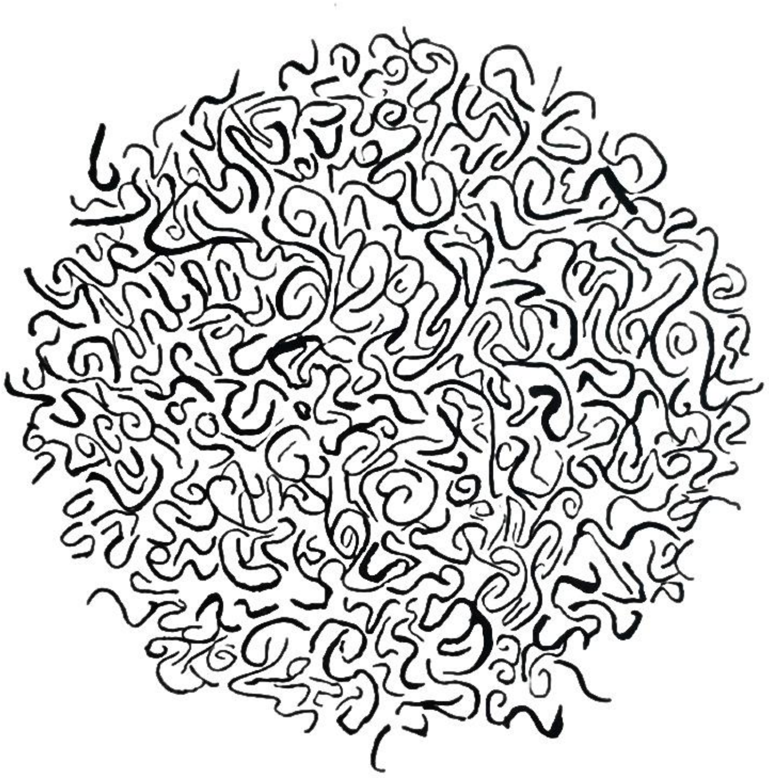

“Apart from such human artifacts as buildings and roads (especially Roman and American roads), our universe, including ourselves, is thoroughly wiggly. Its features are wiggly in both shape and conduct. Clouds, mountains, plants, rivers, animals, coastlines—all wiggle. They wiggle so much and in so many different ways that no one can really make out where one wiggle begins and another ends, whether in space or in time. […] However much we divide, count, sort, or classify this wiggling into particular things and events, this is no more than a way of thinking about the world: it is never actually divided.”

-Alan Watts, The Book on the taboo against knowing who you are, 1966

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English abstract

Species diversity is a key concept in ecological research. However, being scale-dependent and multidimensional, its quantification is often elusive and ambiguous. This dissertation develops new quantitative methods for the measurement of species diversity in the light of incomplete sampling and abundance variation. Species diversity is considered in terms of three components underlying diversity scaling: 1) the species abundance distribution, 2) the total the number of individuals, and 3) the spatial distribution of species (e.g. intraspecific spatial aggregation). By applying the new methods to datasets documenting latitudinal and elevational gradients of diversity, this dissertation contributes to a more nuanced understanding of these patterns. The new approaches of this dissertation form a methodologically coherent framework for the quantification of species diversity, applicable to a wide range of ecological questions in space and time.

Keywords: Species diversity, individual-based rarefaction, effective number of species, more-individual effect, beta-diversity, elevational diversity gradient, latitudinal diversity gradient, sampling effects, diversity scaling

Deutsche Zusammenfassung

Die Artendiversität ist ein Schlüsselbegriff in der ökologischen Forschung. Da sie jedoch skalenabhängig und multidimensional ist, ist ihre Quantifizierung oft schwer fassbar und mehrdeutig. In dieser Dissertation werden neue quantitative Methoden zur Messung der Artendiversität unter Berücksichtigung unvollständiger Stichproben und Abundanzschwankungen entwickelt. Die Arbeit orientiert sich an drei Komponenten, die der Skalierung von Diversität zugrunde liegen: 1) die Artenabundanzverteilung, 2) die Gesamtzahl der Individuen und 3) die räumliche Verteilung der Arten. Durch die Anwendung der neuen Methoden auf Datensätze über Diversitätsveränderungen entlang von Breiten- und Höhengradienten trägt diese Dissertation zu einem differenzierteren Verständnis dieser Muster bei. Die neuen Ansätze dieser Dissertation bilden einen methodisch kohärenten Rahmen für die Quantifizierung der Artendiversität, der auf ein breites Spektrum ökologischer Fragen in Raum und Zeit anwendbar ist.

Schlüsselwörter: Artenvielfalt, effektive Artenzahl, Mehr-Individuen-Effekt, Beta-Diversität, Höhengradienten, Breitengradienten, Stichproben-Effekte, Diversitätsskalierung

Chapter 1 – General introduction

Species diversity, that is the number of species in an area and the distribution of their abundances, is a concept at the very heart of ecology. Many longstanding and important research questions approach the idea from a range of different perspectives: How is species diversity distributed around the globe (Gaston, 2000; Macarthur, 1965; Rosenzweig, 1995)? What are the eco-evolutionary processes that produce and maintain patterns of species diversity at different spatial scales (Currie, 1991; Hagen, 2022; Hawkins et al., 2003; Keil & Chase, 2019)? What is the role of species diversity in the functioning of ecological systems (Hooper et al., 2005; van der Plas, 2019)? How do species assemblages change over time (Blowes et al., 2019; Dornelas et al., 2014)? How do we as humans depend on it and what, in turn, is our anthropogenic impact on the fate of species diversity (Díaz et al., 2019; Isbell et al., 2022)? Overall, species diversity is certainly one of the most commonly reported variables in empirical studies. Furthermore, it is the subject of many fundamental ecological laws and theories, such as the species-area relationship, the theory of island biogeography (MacArthur & Wilson, 1967), niche theory (Chase & Leibold, 2003), neutral theory (Hubbell, 2001), metabolic theory of ecology (Brown et al., 2004) and meta-community theory (Leibold et al., 2004) – just to name a few.

Despite its paramount importance for ecological research, the concept of species diversity is inherently elusive and ambiguous, and ecologists have long struggled with its operationalization and measurement (Chase & Knight, 2013; Gotelli & Colwell, 2001; Hill, 1973; Hurlbert, 1971; Roswell et al., 2021). For example in her 1988 book on this topic, Magurran compares diversity with an optical illusion, stating that “the more it is looked at, the less clearly defined it appears to be and viewing it from different angles can lead to different perceptions of what is involved.” (Magurran, 1988). It is hard to quantify species diversity because it is a multivariate construct that encompasses the occurrences and abundances of multiple species (Chase et al., 2018). There is no one diversity metric that captures all its aspects in a single value, while at the same time there is an overwhelming multitude of complicated and often uninterpretable diversity metrics available to choose from (Gotelli & Chao, 2013). Adding to the difficulty, all measures of species diversity are inherently scale-dependent, which means that their values change non-linearly with area, sampling effort and the number of individuals captured in a sample (Gotelli & Colwell, 2001; McGill, 2010).

In the light of this multidimensional and scale-dependent character, species diversity is, thus, ideally viewed as a complex scaling relationship (e.g. a species-area curve or a species accumulation curve) rather than a single number (Chase et al., 2018). Although such a scale-explicit conception of diversity is great from a theoretical perspective, for most practical purposes it is, however, just not feasible or useful. First, most diversity data are simply only available at one spatial scale (or sometimes two at best). Second, even if we have all the information to describe diversity-scaling relationships in detail, as soon as we want to compare, generalize and synthesize patterns from different places or systems, we usually have to summarize these relationships into a number of simpler interpretable key aspects. Thus, the central challenge of measuring diversity is identifying a set of simple and complementary diversity measures that meaningfully summarize the complex diversity-scaling relationship underlying any diversity observation.

The exact shape of diversity scaling relationships - and along with it the observed diversity value at any given scale - can be understood to result from the interplay of three mutually-dependent broad components of diversity scaling (Chase & Knight, 2013; He & Legendre, 2002; McGill, 2011): 1) the species abundance distribution (SAD) of a regional species pool (i.e. the total number of species in a region and their relative and absolute frequencies), 2) the total abundance (i.e. the number of individuals [N]) supported by the environment, and 3) the spatial distribution of species in the region (e.g. intraspecific aggregation and interspecific associations). Recent work has suggested that these components of diversity scaling can serve as meaningful cornerstones for describing inherently scale-dependent and multidimensional diversity patterns in practical terms (Chase et al., 2018; McGlinn et al., 2019). For example, similar patterns of species richness (i.e. the number of species observed in an area) can manifest in qualitatively very distinct ways, depending on the underlying patterns in the SAD, the number of individuals and spatial aggregation. This is illustrated by the three diversity gradients in Figure 1 A that show similar patterns of decreasing local species richness (i.e. α-diversity) but different accompanying patterns of SAD, N, and spatial aggregation. By quantifying diversity in terms of these components, we can paint a more nuanced picture of diversity patterns than by considering single-scale species richness alone (Blowes et al., 2017; Chase et al., 2018).

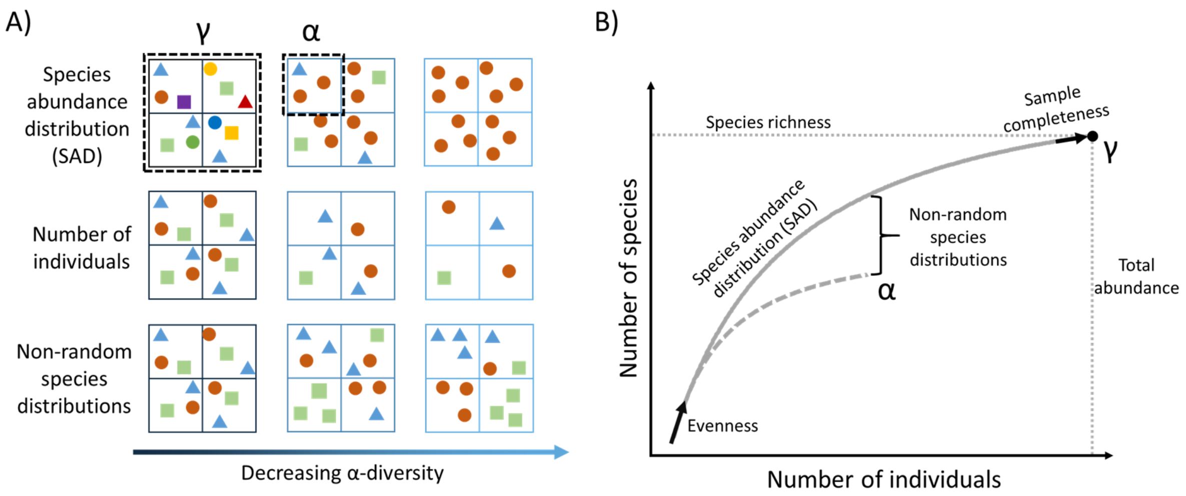

Figure 1: The components of diversity scaling and their link to the individual-based rarefaction curve. A) similar patterns of local species richness (alpha diversity) can be underlain by different patterns in the regional SAD, the total number of individuals and spatial distribution of species (e.g. intraspecific spatial aggregation). B) Different parts of the individual based rarefaction (IBR) curve at α (i.e. local) and γ (i.e. regional) scales reflect these diversity components. The solid grey line shows the γ scale; the dashed grey line shows the α scale.

Patterns in the diversity components also relate to different ecological processes and hypotheses, which may help with the linking of empirical patterns and mechanisms (Gooriah et al., 2021; Blowes et al., 2022). For example, variation in total abundance, reflecting resource or energy availability, is often invoked as a simple explanation for observed differences in species richness (Colwell et al., 2012; Srivastava & Lawton, 1998; Storch et al., 2018; Wright, 1983). Such abundance-related mechanisms are also referred to as the “passive sampling effect” or the “more-individual hypothesis”, and I return to them many times throughout this dissertation. Similarly, patterns of intraspecific spatial aggregation are thought to reflect small-scale community assembly processes based on species’ niches (e.g. environmental heterogeneity) or dispersal limitation, whereas patterns in the regional SAD are believed to capture processes that operate on larger scales (e.g. speciation, extinction, climatic constraints and plate tectonics) (Currie, 1991; Kraft et al., 2011).

In the last decade, there has been an ongoing debate on how these latter two components, in particular, contribute to differences in diversity scaling along biogeographic gradients (e.g. latitudinal gradients) through their influence on β-diversity (Kraft et al., 2011; Tuomisto & Ruokolainen, 2012; Ulrich et al., 2017; Xu et al., 2015). Measures of β-diversity (over-)simplify diversity scaling relationships into a single number, as they describe the mathematical relationship between a regional-scale diversity (i.e. γ-diversity) and a mean local-scale diversity (i.e. α-diversity), for example as a simple ratio (β=γ/α) (Whittaker, 1960). Although β-diversity is conceptually appealing, its interpretation remains highly ambiguous (Tuomisto 2010a, 2010b, Anderson et al. 2011), because - just like most other diversity measures - β-diversity confounds the abovementioned components of numbers of individuals, the species abundance distribution and within species aggregation. In chapter 2, I discuss these issues in detail and I develop a β-diversity metric that responds to changes in spatial aggregation but remains unaffected by changes in the species pool size.

The basis for this and the other quantitative approaches presented in this dissertation is the individual-based rarefaction (IBR) curve. Rarefaction has long been a popular tool for the quantification of species diversity (Chao & Jost, 2012; Gotelli & Colwell, 2001; Hurlbert, 1971), but more recent work has specifically emphasized its utility for the disentanglement of the three components of diversity scaling through complementary metrics derived from the IBR curve (Chase et al., 2018; McGlinn et al., 2019; Olszewski, 2004). IBR curves describe the non-linear scaling relationship between the number of individuals in a sample and expected species richness (i.e., rarefied richness) (Fig 1B). Thus, by comparing IBR curves of different samples, one can address differences in total abundance (i.e. more-individual effects). The shape of the IBR curve is determined by the SAD of the regional species pool such that for any constant number of species, samples with higher evenness produce steeper curves. At the same time, the slope of the curve is also an indication of sample completeness; steep slopes at the endpoint of the curve suggest that there are many “unseen” species, whereas curves that asymptote indicate high sample completeness (Chao & Jost, 2012). Finally, by constructing IBR curves from samples at two or more nested spatial scales, we can assess intraspecific spatial aggregation (Chase et al., 2018; Dauby & Hardy, 2012; McGlinn et al., 2019; Olszewski, 2004). If species are distributed randomly among samples (i.e., there is no aggregation), the α-and γ-scale IBR curves sit on top of each other, whereas deviations between the curves indicate nonrandom spatial structure (Fig. 1B). Making use of these properties, diversity metrics derived from different parts of the IBR curve capture the components of diversity scaling in a complementary way (Blowes et al., 2022; Chase et al., 2018; McGlinn et al., 2018).

However, due to variable numerical constraints along the IBR curve, different diversity metrics and their effect sizes are usually not directly quantitatively comparable (Dauby & Hardy, 2012). In practice, this makes it difficult to assess the relative contributions of the three diversity components towards an observed diversity pattern at a given scale. What are, for example, the relative contributions of more individual effects and changes in the regional SAD to a diversity pattern at a given scale (such as a latitudinal diversity gradient)? In Chapter 3 of this dissertation, I delve into this question and develop a quantitative approach for dissecting the two diversity components. Using the effective number conversion of the IBR curve (Dauby & Hardy, 2012), I show how to decompose the total diversity of a sample into two additive components: One component is affected by the SAD and its changes, and the other is affected by the number of individuals (N) and associated passive sampling effects. Using a case study of latitudinal diversity gradients in trees and reef fish, I illustrate how such a quantitative dissection allows for a more nuanced comparison of multidimensional diversity patterns.

In the fourth Chapter, I apply the newly developed methods in a synthesis study of elevational diversity gradients. Elevational diversity gradients are among the most iconic patterns of biodiversity and they are often considered “natural laboratories” that provide insights into community assembly processes (Rahbek et al., 2019; Sanders & Rahbek, 2012; Tito et al., 2020). In the last decades, several studies have reviewed the relationship between altitude and species richness (e.g. McCain, 2005, 2009, 2010; McCain & Grytnes, 2010; Rahbek, 1995), but so far there has not been a quantitative synthesis using abundance-based measures of diversity that go beyond species richness. Therefore, for this study, I compiled publically available datasets to analyze the role of more individuals and variation in the SAD for elevational gradients of species diversity. I demonstrate that overall processes beyond passive sampling seem to underlie decreasing elevational diversity patterns.

Finally, in Chapter 5 I tie everything together. I show how the findings of the previous chapters are connected, discuss them in the context of the recent and not so recent literature, and outline promising directions for future research.

With this dissertation, I expand our understanding of species diversity as a multidimensional, scale-dependent phenomenon, and introduce new, more accurate tools for quantifying its variation. May this be useful to anyone who counts living things!

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Chapter 2 – Using coverage-based rarefaction to infer non-random species distributions

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METHODS, TOOLS, AND TECHNOLOGIES

Using coverage-based rarefaction to infer non-random species distributions

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Abstract. Understanding how species are non-randomly distributed in space and how the resulting spatial structure responds to ecological, biogeographic, and anthropogenic drivers is a critical piece of the biodiversity puzzle. However, most metrics that quantify the spatial structure of diversity (i.e., community differentiation), such as Whittaker's β-diversity, depend on sampling effort and are influenced by species pool size, species abundance distributions, and numbers of individuals. Null models are useful for identifying the degree of differentiation among communities due to spatial structuring relative to that expected from sampling effects, but do not accommodate the influence of sample completeness (i.e., the proportion of the species pool in a given sample). Here, we develop an approach that makes use of individual- and coverage-based rarefaction and extrapolation, to derive a metric, β_C, which captures changes in intraspecific aggregation independently of changes in the species pool size. We illustrate the metric using spatially explicit simulations and two case studies: (1) a re-analysis of the "Gentry" plot data set consisting of small forest plots spanning a latitudinal gradient from North to South America and (2) comparing a large plot in high diversity tropical forests of Barro Colorado Island, Panama, with a plot in a lower diversity temperate forest in Harvard Forest, Massachusetts, USA. We find no evidence for systematic changes in spatial structure with latitude in these data sets. As it is rooted in biodiversity sampling theory and explicitly controls for sample completeness, our approach represents an important advance over existing null models for spatial aggregation. Potential applications range from better descriptors of biogeographic diversity patterns to the consolidation of local and regional diversity trends in the current biodiversity crisis.

Key words: β-deviation; β-diversity; coverage; null models; rarefaction; sample completeness; spatial aggregation; species abundance distribution; species pool; turnover.

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INTRODUCTION

Species are non-randomly distributed across the globe, and understanding spatial patterns of species diversity from ecological samples remains a central challenge (Gaston 2000, McGill 2011, Worm and Tittensor 2018). Spatial structure in species diversity (e.g., species turnover from site to site) is typically quantified by one or more metrics of compositional dissimilarity or spatial β-diversity (Anderson et al. 2011). Measures of β-diversity offer a mathematical link between local (i.e., α) and regional (i.e., γ) species diversity and can, for example, shed light onto the metacommunity processes that shape biological assemblages (Chase and Myers 2011) inform biodiversity conservation (Socolar et al. 2016), and help understand the provisioning of ecosystem functions and services (Mori et al. 2018).

Although β-diversity is conceptually appealing, its quantification and interpretation are often ambiguous (Tuomisto 2010*a*, *b*, Anderson et al. 2011). Whittaker's (1960) multiplicative β-diversity (γ/α), for example, is commonly thought to represent the sort of community differentiation that arises due to non-random distributions of species (e.g., species turnover or intraspecific spatial aggregation). However, this and other measures of β-diversity are also influenced by the size and number of samples, the size of the regional species pool, the shape of the regional species abundance distribution (SAD), and the number of individuals captured by the samples (McGill 2011, Chase and Knight 2013, Chase et al. 2018). This makes it a challenge to compare and interpret patterns of β-diversity and related measures along biogeographic gradients (e.g., Kraft et al. 2011). To disentangle the effect of spatial aggregation from the non-spatial components that influence β-diversity (SAD or relative proportion of rare species, species pool size), empirical studies have frequently adopted null-modeling approaches that compare the observed patterns against a null expectation that simulates spatial randomness by shuffling individuals among sites (Chase et al. 2011, Kraft et al. 2011). However, the exact formulation of the null expectation and its deviation (β-deviation) remains debated (Kraft et al. 2012, Qian et al. 2012, Tucker et al. 2016, Mori et al. 2018, Xing and He 2021). In particular, the null model approach has been criticized because it overlooks the influence of the completeness of the samples (Ulrich et al. 2017, Sreekar et al. 2018).

Much of the ambiguity surrounding measures of β-diversity and its null expectations can be understood in terms of sampling effects and sample completeness (i.e., the proportion of species in the species pool captured by sampling). For instance, regions with large species pools are expected to exhibit high β-diversity simply because local samples only capture a small and incomplete portion of the total diversity; this can lead to strong, but spurious differentiation among local samples (Chase and Myers 2011, Kraft et al. 2011). This is not to say that this kind of sample differentiation is not meaningful, but it reflects the species pool (or the inability of local samples to sample it) rather than non-random species distributions. Similarly, sampling effects can "inflate" metrics of β-diversity when there are many rare species in an assemblage, or when the total community density is relatively low (i.e., widespread species remain undetected in most samples) (Barwell et al. 2015). Although such sampling effects are ubiquitous in ecological studies (Colwell and Coddington 1994, Gotelli and Colwell 2001), sampling theory is not well developed with respect to β-diversity (Wolda 1981, Beck et al. 2013). For example, Chao and Chiu (2016) developed a framework to unify different approaches to community differentiation, but they state clearly that their approach ignores such sampling issues. There have also been attempts to develop asymptotic β-diversity metrics (Chao et al. 2005), but these have been found to show strong biases when tested on simulated and empirical data (Cardoso et al. 2009, Beck et al. 2013). While rarefaction-based approaches are commonly used to address sampling effects at a single scale by standardizing diversity to a common number of individuals (Gotelli and Colwell 2001) or to equal levels of sample completeness (Chao and Jost 2012), these approaches have been rarely applied to concepts related to β-diversity (but see Olszewski 2004, Dauby and Hardy 2012, Stier et al. 2016, Chase et al. 2018). This is despite the fact that the null models used in detecting deviations from random expectations in β-diversity(e.g., Kraft et al. 2011, Xing and He 2021) are based on largely similar concepts (i.e., difference between observed and expected measures of diversity).

In what follows, we consider non-random spatial distributions through the lens of the individual-based rarefaction curve and combine existing approaches (Chase et al. 2018, McGlinn et al. 2019) with coverage-based standardization.

Specifically, we compare rarefaction curves taken from subsets of samples (i.e., an α-scale curve) to those from the entire set of samples (i.e., a γ-scale rarefaction curve), using a constant γ-scale coverage (i.e., an estimate of sample completeness). From this, we obtain a metric, which we call β_C, that estimates the degree of spatial structure in the assemblage independently of the species pool size and the SAD. We emphasize that our goal here is not to develop a better measure of β-diversity per se, as it is true that Whittaker's β-diversity and relatives have many useful properties for discerning biodiversity scaling (e.g., Jost 2007, Tuomisto 2010*a*, *b*, Chao and Chiu 2016). Instead, our goal is to develop a measure that allows us to discern the magnitude of spatial structuring within a given regional assemblage. Building on rarefaction and sampling theory has the advantage that we can evaluate sample completeness and bypass the shuffling algorithms and estimates of beta-deviation inherent to previous null-modeling approaches. We test our method on simulated spatial point patterns with different degrees of spatial structure (intraspecific spatial aggregation) and varying species pool sizes and apply it to two empirical data sets to examine variation in spatial structure along a latitudinal gradient of tree diversity.

INDIVIDUAL-BASED RAREFACTION AND EXTRAPOLATION (IBRE)

Our approach is based on individual-based rarefaction and extrapolation (IBRE), which is a common method to standardize species richness estimates (Hurlbert 1971, Gotelli and Colwell 2001, Chao and Jost 2012). IBRE curves describe the nonlinear scaling relationship between the number of individuals in a sample and expected species richness (i.e., rarefied richness). The shape of the curve is determined by the size of the species pool and the relative abundances of species in that pool, which is often referred to as the species abundance distribution (SAD, McGill et al. 2007). The slope at any point along the curve is related to the estimated sample completeness for the number of individuals sampled at that point (Chao and Jost 2012). For smaller than observed sample sizes, the expected number of species can be interpolated using the following formula (Hurlbert 1971):

$$S_n = S_{\text{obs}} - \sum_{X_i \geq 1} \frac{\binom{N - X_i}{n}}{\binom{N}{n}} \tag{1}$$

where S_n is the rarefied richness, or the expected number of species for n individuals ($n < N$), S_{obs} is the observed number of species, N is the observed number of individuals in the sample, and X_i is the number of individuals of the ith species.

For larger than observed sample sizes, the expected number of species can be estimated using the following extrapolation formula (Chao and Jost 2012):

$$S_n = S_{\text{obs}} + \widehat{f}_0 \left[1 - \left(1 - \frac{f_1}{N\widehat{f}_0 + f_1}\right)^{n-N}\right] \tag{2}$$

where $\widehat{f}_0$ is the estimated number of unseen species, estimated as follows:

$$\widehat{f}_0 = \begin{cases} \dfrac{(N-1)}{N} \dfrac{f_1^2}{2f_2}, \text{ if } f_2 > 0 \\ \dfrac{(N-1)}{N} \dfrac{f_1(f_1 - 1)}{2}, \text{ if } f_2 = 0 \end{cases} \tag{3}$$

and f_1 and f_2 are the observed numbers of singletons and doubletons (i.e., species represented by one or two individuals), respectively. Extrapolation of species richness is considered unbiased, though only recommended for sample sizes up to two times the observed sample size (Chao et al. 2014).

SPATIAL STRUCTURE THROUGH THE LENS OF THE IBRE CURVE

By constructing IBRE curves from samples at two or more nested spatial scales, we can assess intraspecific spatial aggregation (Olszewski 2004, Dauby and Hardy 2012, Chase et al. 2018, McGlinn et al. 2019). Like most classical approaches to diversity partitioning, we define α-diversity as the mean number of species within a given sample or subset of localized samples, and γ-diversity as the total number of species from multiple pooled samples or local subsets of samples (Tuomisto 2010*a*). Accordingly, the α-scale IBRE curve is derived by calculating the

IBRE curve from each individual sample and then averaging the all samples (${}^{\alpha}\overline{S_n}$) while the γ-scale curve consists of S_n values calculated from the pooled sample (${}^{\gamma}\overline{S_n}$). The α-scale is influenced by turnover (i.e., spatial structure) among samples within the assemblage, whereas the γ-scale breaks up any spatial structure by randomly accumulating individuals from all samples. If species are distributed randomly among samples (i.e., there is no aggregation), the α- and γ-scale IBRE curves sit on top of each other (Fig. 1). Downward and upward deviations of the α-scale curve, then, would be interpreted as intraspecific aggregation and overdispersion, respectively (Chase et al. 2018, McGlinn et al. 2019). The γ-scale IBRE is conceptually very similar to abundance-based null expectations (Kraft et al. 2011), but it uses an analytical formula rather than a shuffling algorithm. Furthermore, rather than comparing the observed β-diversity to a null distribution of β-diversity, it directly compares the observed α-scale IBRE curve to the null expectation given by the γ-scale IBRE curve.

Using IBRE curves (only interpolation shown for simplicity), Fig. 1 illustrates how β-diversity of a reference assemblage (Fig. 1A) responds to changes in the size of the species pool (Fig. 1B), the numbers of individuals (Fig. 1C), and intraspecific spatial aggregation (Fig. 1D). Whittaker's β-diversity ($\beta = \frac{\gamma}{\alpha}$) is represented as the height ratio of the two curves at the respective right-hand end of the curves (dashed horizontal lines). In each of the four examples, $\beta > 1$, but for very different underlying reasons. Only the assemblage underlying Fig. 1D exhibits spatial turnover in species composition (due to aggregation). In the other cases (A-C), differentiation only emerges due to a sampling effect (i.e., a

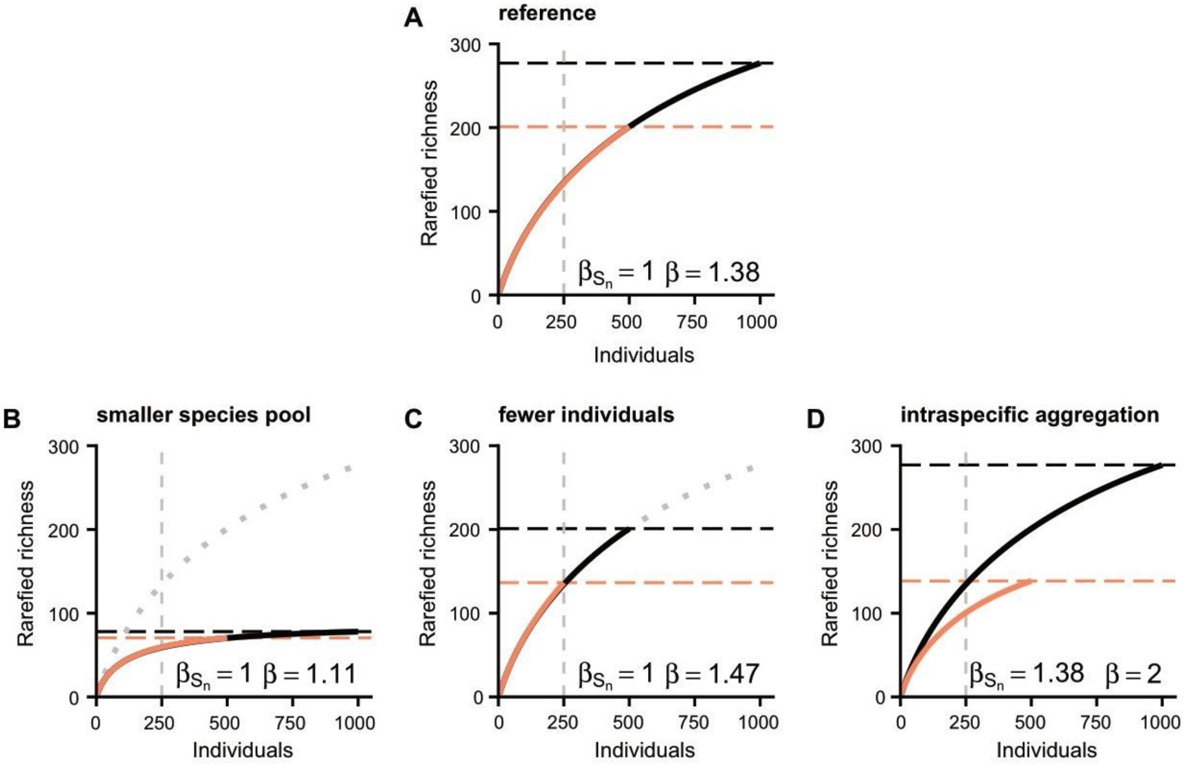


Fig. 1. Examples of two-scale individual-based rarefaction curves for (A) a hypothetical species pool size of 450, and how they respond to, (B) reduced species pool size/altered SAD (species pool size of 80), (C) reduced numbers of individuals, (D) and changes to patterns of within species aggregation. Orange curve: α-scale, black curve: γ-scale. Dashed lines represent observed species richness at α- and γ-scales, and Whittaker's β-diversity (β) can be illustrated as the height ratio of the two. β_{S_n} values are calculated for n = 250 individuals on all panels (dashed vertical lines). Dotted gray curve in panel C: reference curve (from A) to aid comparison.

"more-individuals" effect between the α-scale and γ-scale).

Due to the nonlinear shape of the IBRE curve, the sampling effect depends on the regional SAD (Fig. 1B) and the number of individuals sampled (Fig. 1C). Chase et al. (2018) suggested that when calculated at a common number of individuals (n), the ratio of rarefied richness (S_n) calculated between the γ- and α-scales, termed β_{S_n}, could provide an indication of the degree of intraspecific aggregation, or non-randomness in the distribution of species in the assemblage, independent of any sampling effect (see also McGlinn et al. 2019). β_{S_n} is related to metrics developed by Olszewski (2004) and Dauby and Hardy (2012) who also assess the differences between γ and α IBRE curves. When assemblages have a random spatial structure, β_{S_n} is expected to equal 1 regardless of species pool and sample size (Fig. 1A-C). Conversely, β_{S_n} values larger than 1 reflect spatial aggregation or species turnover among sites in the region (Fig. 1 D).

While the deviation between α- and γ-scale IBRE curves (i.e., $\beta_{S_n} \neq 1$ is due to spatial structure, its magnitude is contingent on the value of n and the shape of the curves (i.e., the size and evenness of the species pool). Thus, as we will illustrate below, β_{S_n} is biased when comparing the degree of aggregation among regions where species pools and shapes of the γ-scale IBRE curves change (e.g., along biogeographical gradients). To visualize this problem, consider two assemblages each composed of two patches, but which differ in the size of their regional species pool (500 vs. 100 species Fig. 2A, B, respectively). Supposing that both assemblages have complete species turnover between their respective patches, Fig. 2 shows the IBRE curves that we would expect if we sampled 500 individuals from each patch in the large (Fig. 2A) and small (Fig. 2B) species pools. Note how the γ-curve from the small species pool is much closer to its asymptote than the one from the large species pool (slope of gray tangential lines). This

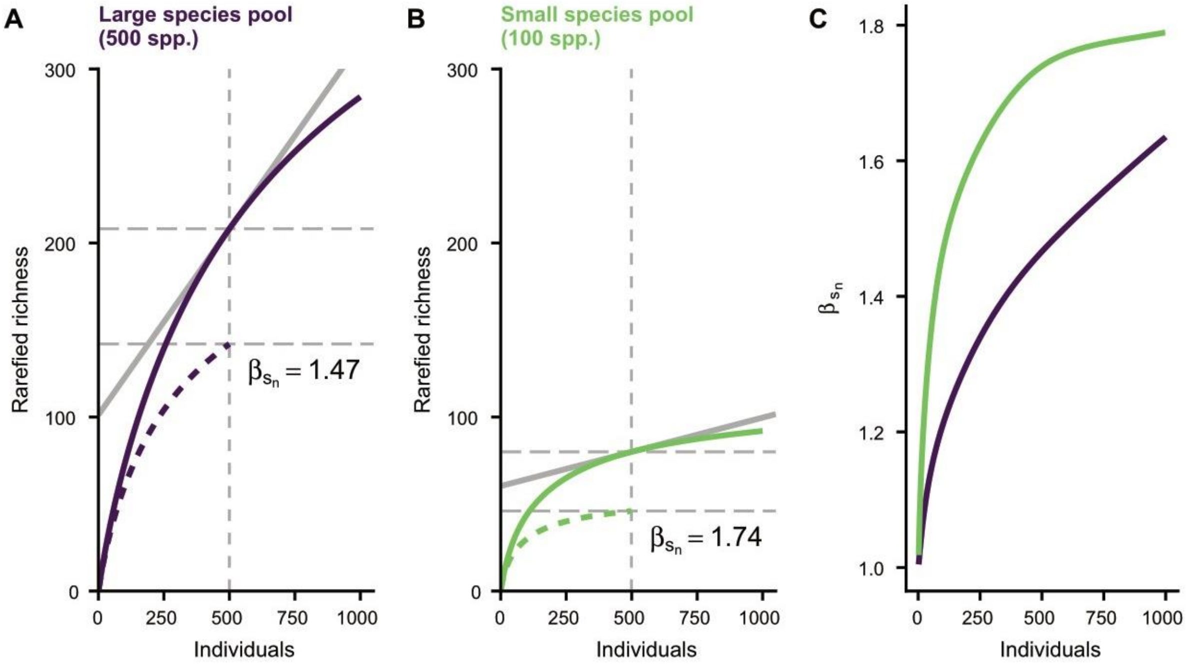


Fig. 2. β_{S_n} is affected by species pool size in aggregated communities. Two-scale IBRE curves for (A) a large species pool and (B) a small species pool. Solid curve: γ-scale; dashed curve: α-scale; dashed vertical gray line: number of individuals (n = 500) used for the calculation of β_{S_n} (i.e., the ratio of the horizontal dashed lines). Gray solid line shows the slope of the γ-scale IBRE that relates to sample coverage (the steeper the slope of this line, the less complete the sample). (C) β_{S_n} plotted as a function of the corresponding sample size (n).

difference in completeness has implications for the values of β_{S_n}. Although both assemblages are maximally and equally structured at the patch scale, the relative deviation between α and γ is substantially higher in the small species pool (indicated by β_{S_n}). Asymptotically, both assemblages have a theoretical β-diversity of 2 (i.e., complete turnover), but at any common sample size, β_{S_n} differs between them due to the difference in sample completeness that is associated with species pool size (Fig. 2C).

COVERAGE-BASED RAREFACTION AND EXTRAPOLATION

To account for the differences in species pool size and sample completeness, we extend β_{S_n} to include the concept of coverage-based rarefaction (Chao and Jost 2012). Sample coverage is a measure of sample completeness that ranges from 0 to 1 and refers to the "proportion of the total number of individuals in a community that belong to the species represented in the sample" (Chao and Jost 2012). Sample coverage depends on the sample size and the species abundance distribution of the underlying assemblage. It can be estimated from the number of rare species in a sample (Good 1953, Chao and Shen 2010). As it is directly related to the steepness of the IBRE curve, expected coverage can also be estimated for any sample size along the curve using the following equations (Chao and Jost 2012).

$$C_n = \begin{cases} 1 - \sum_{X_i \geq 1} \dfrac{X_i}{N} \dfrac{\binom{N-X_i}{n}}{\binom{N-1}{n}}, & \text{for interpolation } (n<N) \\ 1 - \dfrac{f_1}{N}\left[\dfrac{(N-1)f_1}{(N-1)f_1+2f_2}\right]^{n-N+1}, & \text{for extrapolation } (n>N) \end{cases} \tag{4}$$

where C_n is the expected coverage for a subsample of sample size n. N is the total number of individuals in the sample, X_i is the number of individuals of the ith species, and f_1 and f_2 are the numbers of singletons and doubletons.

For coverage-based standardization, Eq. 4 can be solved numerically to determine how many individuals, n, are necessary to obtain a given target coverage, C_{target}. This is computed by calculating C_n for every possible n and choosing the one that minimizes the difference between C_n and C_{target}. Subsequently, IBRE can be used to standardize the diversity estimate to a sample size of n, and thus the desired coverage level C_{target} (Hsieh et al. 2016).

INTRODUCING β_C

By calculating β_{S_n} for equal γ-scale coverage, we can resolve the species pool dependence when making comparisons across assemblages. Specifically, rather than keeping sample size (n) constant when comparing across assemblages, we instead maintain a consistent sample coverage at the γ-scale (C_{target}) and refer to β_{S_n} standardized by sample coverage as β_C. Fig. 3 illustrates this approach using the same example with large (Fig. 3A) and small (Fig. 3B) species pools. By allowing n to vary between scenarios so that we maintain a constant γ-scale coverage (indicated by the slope of the tangential lines), the resulting pair of β_C values become practically identical (compare with Fig. 2), which accurately reflects that both scenarios are equally aggregated at the patch scale. The advantage of standardizing γ-scale coverage becomes particularly clear when we consider the entire scaling relationship of β_C. If we quantify β_C for every possible value of n and plot them against γ-scale expected coverage, the values from large and small species pool fall on approximately the same line and the species pool dependence vanishes (Fig. 3C, compare with Fig. 2C).

To compare β_C across multiple assemblages (e.g., with different species pools), we suggest the following protocol that makes use of interpolation and extrapolation.

1. Determine the appropriate target coverage value C_{target} for the standardization:
    1.1. For each assemblage j, determine the smallest number of individuals observed at the α-scale and call it $N_{\min_j}$.
    1.2. Using Eq. 4, estimate the expected γ-scale coverage C_n corresponding to $N_{\min_j}$ individuals, or up to $2N_{\min_j}$ individuals if you wish to use extrapolation (Chao et al. 2014).
    1.3. Let C_{target} be the smallest of the C_n values across all assemblages.

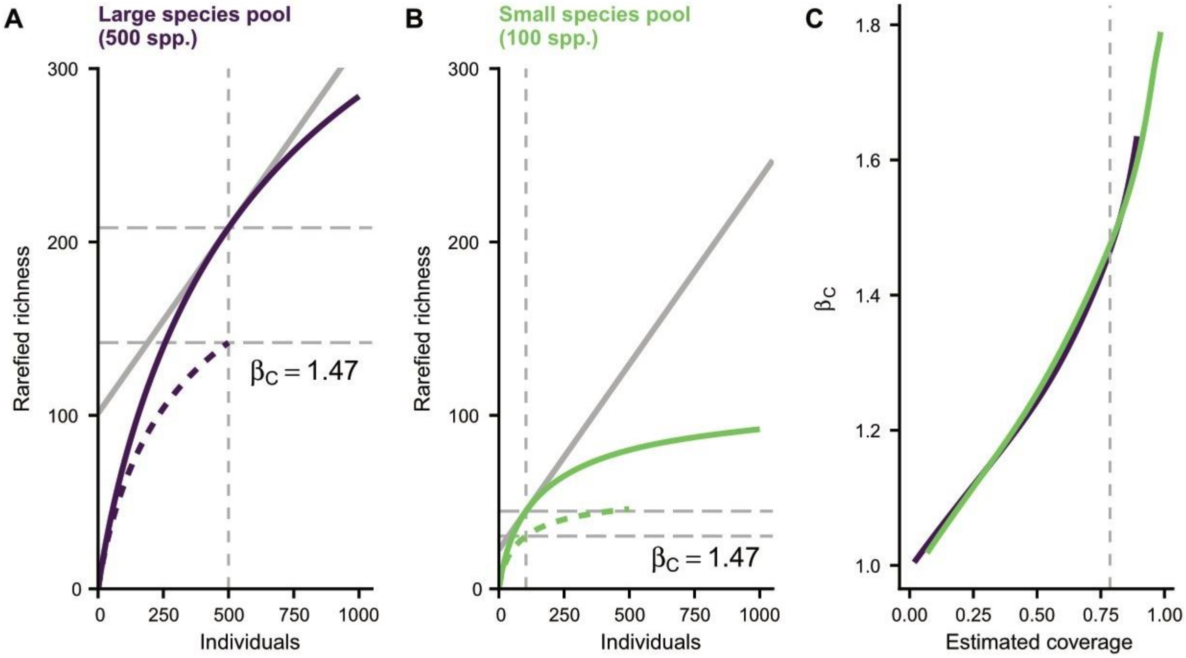


Fig. 3. β_C is unaffected by species pool size in aggregated communities (compare with Fig 2). Two-scale IBRE curves for (A) a large species pool and (B) a small species pool. Solid curve: γ-scale; dashed curve: α-scale; dashed vertical gray line: number of individuals used for the calculation of β_{S_n} (i.e., the ratio of the horizontal dashed lines). Gray solid line shows the slope of the γ-scale IBRE that relates to sample coverage ($C = 0.79$ in both panels). (C) β_C plotted as a function of expected coverage calculated at the γ-scale. Dashed line marks the coverage value of 0.79 used in other panels.

2. Calculate β_C:

   2.1. For each assemblage, use the inverse of Eqn 4 to estimate the sample size n_j corresponding to a γ-scale coverage of C_{target}. Exclude all assemblages for which $n_j \leq 1$.

   2.2. Standardize γ- and α-scale species richness to n_j individuals (using IBRE) to get ${}^{\gamma}S_{n,j}$ and ${}^{\alpha}\overline{S_{n,j}}$.

   2.3. Calculate β_C as follows:

$$\beta_{c_j} = \frac{{}^{\gamma}S_{n,j}}{{}^{\alpha}\overline{S_{n,j}}} \tag{5}$$

We implemented this procedure in an R package available on GitHub (https://github.com/t-engel/betaC) and archived on Zenodo (https://doi.org/10.5281/zenodo.4727184). It provides the function "C_target" that can be used for steps 1.1 and 1.2, and the function "beta_C" that carries out step 2.

This approach requires spatially replicated samples with abundance data (i.e., site-by-species matrices with abundance data), so that one can define at least two nested sampling scales (α and γ). We assume that the sampling design is standardized across all assemblages. This means there should be a consistent number of samples per assemblage and every sample should have the same effort (e.g., plot size and trap nights). Furthermore, we assume a consistent spatial extent at the γ-scale. If the number of samples, or their spatial extent changes from one assemblage to the next, users should take a spatially constrained subset of the samples to keep extents as consistent as possible.

Like most measures of community differentiation, β_C does not have an analytical variance estimator because there are no replicates at the γ-scale. Nevertheless, such variance is often desired, for example, when comparing spatial structure among different regions. To do so, we recommend calculating a distribution of β_C for repeated random subsets of the samples. For example, one could use a Jackknife approach (i.e., systematically leaving out one sample at a time), use pairwise comparisons of samples, or comparisons among larger subsets of samples. While such variance can help to contextualize the observed values of β-diversity, caution should be taken because these calculations incorporate some degree of non-independence. Nevertheless, we provide an R function that carries out such resampling procedures for any number of samples (i.e., "betaC::beta_stand").

PROOF OF CONCEPT USING SIMULATIONS

To test the properties of β_C, we simulated spatially explicit assemblages that varied in the size of the species pool and the degree of intraspecific aggregation using multivariate spatial point patterns. We used the R package mobsim (May et al. 2018) to carry out the simulations. Each simulated assemblage had 4000 individuals drawn from a lognormal SAD that was parameterized with a given species pool size, and a coefficient of variation equal to one. Then, we used the Thomas cluster process to distribute individuals in space, varying the degree of intraspecific spatial aggregation through the parameter that determines the number of conspecific clusters. The simulation was parameterized in a full-factorial design, where the species pool size encompassed every integer between 10 and 500, and the number of clusters was set to 1 (i.e., extreme intraspecific aggregation), 4, 10, and 20. To include a level that had no within species aggregation, we also implemented a random Poisson process to simulate completely random spatial distributions for species. Each combination of species pool and aggregation was replicated 3 times yielding a total of 7365 simulated communities. To sample from the regional communities, we placed 4 sample quadrats into each simulated community (Fig. 4A, B). We calculated Whittaker's β ($=\frac{\gamma}{\alpha}$), β_{S_n} and β_C among the four samples and examined their response to changes in species pool size and aggregation. Following the protocol above, C_{target} was set to 0.55 and the sample size for β_{S_n} was 50 individuals. The R code for the simulation is available on Zenodo (https://doi.org/10.5281/zenodo.4727184).

All three indices (Whittaker's β, β_{S_n}, and β_C were influenced by intraspecific community aggregation. Additionally, Whittaker's β and β_{S_n} were affected by the changes in species pool size, whereas β_C was insensitive to this parameter. While both Whittaker's β and β_{S_n} responded to the degree of spatial aggregation and the species pool, they did so in contrasting ways, which is consistent with theoretical expectations (Fig. 4C). For Whittaker's β, the effect of the species pool decreased with increasing aggregation. This reflects that for strongly aggregated species distributions, the samples will always show high turnover regardless of the species pool. In contrast, under random species distributions, "spurious" (i.e., SAD related) sample differentiation is more likely to occur when there are many rare species that only occur in some of the samples (i.e., in large species pools). For β_{S_n}, the effect of the species pool increased with increasing aggregation; as long as species are randomly distributed, β_{S_n} is always one because the α IBRE curve falls onto the γ-scale. However, when there is a deviation between the curves (as a result of aggregation), its magnitude for a given number of individuals (n) depends on the shape of the IBRE curves, which in turn depend on the species pool (Fig. 3). Only β_C captures the spatial structure of the simulated communities independently of the species pool size because, by incorporating sample coverage, it adjust for the species pool dependence.

We examined the robustness of β_C using an alternative SAD (log-series) and by simulating spatial aggregation using the mean displacement length of the Thomas process (Appendix S1). The results were qualitatively similar: β_C, but not Whittaker's β or β_{S_n}, responded to the changes of aggregation independently to changes in the SAD parameter (i.e., Fisher's α). Additionally, we applied the null model by Kraft et al. (2011) to the simulated data and found that the measure of β-deviation, like β_C, responded to the aggregation, but not to the species pool. Spearman's rank correlation between β_C and β-deviation was 97.7% which suggests that both approaches are measuring the same effect (Appendix S2).

EMPIRICAL CASE STUDIES

Next, we applied our approach to two forest data sets with varying species pool sizes. First, we reanalyzed the Gentry Forest plot data set (Gentry 1988, Phillips and Miller 2002). This data

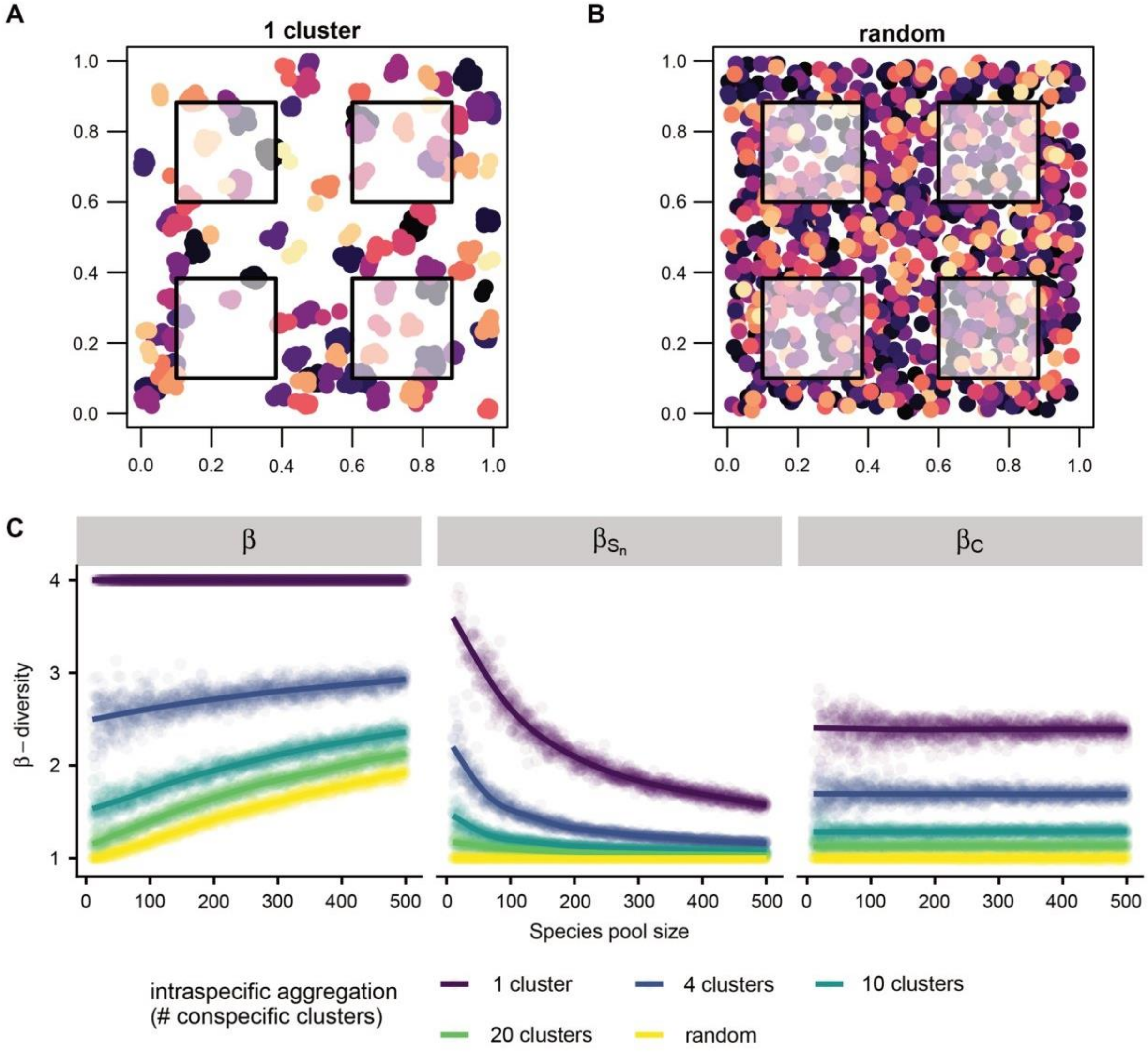
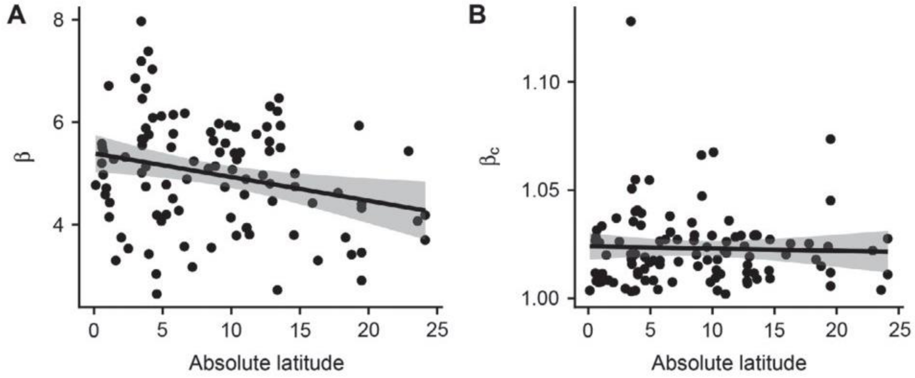
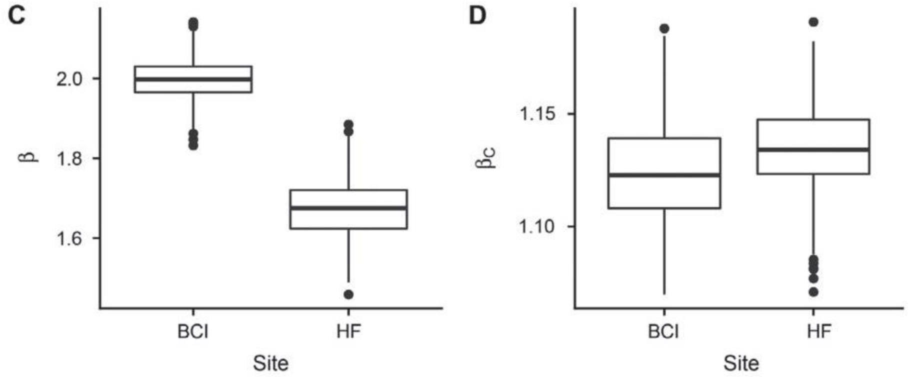


Fig. 4. Simulated assemblages and the response of Whittaker's β, β_{S_n}, and β_C to changes in aggregation and species pool size. (A) Assemblage with extreme intraspecific aggregation (1 cluster per species) and (B) assemblage where species have random spatial distribution. Species pool, SAD, and numbers of individuals are constant between (A) and (B). Squares represent sample quadrats. (C) β-diversity metrics and their response to species pool size and intraspecific aggregation. Dots show the data. Lines show GAM fit to each metric with species pool size as the predictor; the GAM estimated separate smoothers for each level of intraspecific aggregation.

set has frequently been used in the debate on how to formulate appropriate null models for β-diversity and how spatial aggregation varies with latitude (Kraft et al. 2011, Qian and Song 2013, Qian et al. 2013, Xu et al. 2015, Xing and He 2021). We computed Whittaker's β and β_C among the subplots of the sites located in the Americas. As expected from the difference in species pool size along this gradient and shown by previous studies (e.g., Kraft et al. 2011), Whittaker's β declined with latitude (Fig. 5A). In contrast, β_C, which controls for species pool-related sampling effects, showed no significant change along the latitudinal gradient (Fig. 5B). Given this, we conclude that there is no evidence for a change in spatial aggregation along this gradient



Case study 1: Gentry plots ($C_{target} = 0.1$)



Case study 2: BCI vs. HF ($C_{target} = 0.93$)

Fig. 5. Case studies exploring β-diversity along (A, B) a latitudinal gradient of Gentry forest plots and (C, B) comparing Barro Colorado Island (BCI) and Harvard Forest (HF). Both examples show significant changes in Whittaker's β (A, C) while β_C (i.e., β standardized for sample coverage) showed no significant change. Solid lines show simple linear regressions. Boxplots show distribution of values from 1000 redraws of 10 samples, respectively. Whiskers: non-outlier range; box: interquartile range: bar: median.

in these samples. Declines in Whittaker's β with increasing latitude appear to be mostly driven by changes in the size of the regional species pool rather than changes in the spatial structuring of individuals. Importantly, although we come to qualitatively similar results as the abundance-based null models of Kraft et al. (2011) and Xu et al. (2015), our method has the advantage of explicitly incorporating an estimate of sample completeness. Rather than simply shuffling site-by-species matrices, users are confronted with the completeness of their samples as part of the analytical workflow, and prior to interpreting any results. In this case, our analysis provides quantitative evidence for the argument that these types of forest plots may be too small to robustly compare spatial patterns of diversity and any associated differences in community assembly, especially in the tropics (Tuomisto and Ruokolainen 2012). C_{target} is set by the site with the lowest coverage (C_n), which for the Gentry Forest Plot data were $C_{target} = 0.1$. This means that inferences are being drawn from a sample of only approximately 10 percent of the individuals in the assemblage.

For a second case study, we explored a similar question along the latitudinal gradient, but with larger plots, so that a more substantial fraction of the species pool would be sampled. To do so, we compare the spatial structuring of trees within the temperate forest plot at Harvard Forest (HF), in the northeastern United States (Orwig et al. 2015), with the well-studied tropical rainforest plot at Barro Colorado Island (BCI), Panama (Condit et al. 2019). Because the data from HF were from only 35 hectares, we took a 35 ha subsection of the 50 ha plot at BCI and found a considerable difference in γ-diversity; 38 species were present at HF and 217 species were in the analyzed section of BCI. For both locations, we used our resampling approach to calculate a distribution of β-diversity at the scale of ten 1 ha subplots (using 1000 random draws with replacement). Again, we found that Whittaker's β was consistently higher in the more diverse site (BCI). While HF had an expected α-scale coverage of 99%, it was 90% at BCI. By interpolating HF and extrapolating BCI (following the protocol above), we standardized both sites to a target coverage of 0.93 and found no meaningful difference in the corresponding β_C (Fig. 5 D). In short, as with our analyses of the Gentry data above, but with samples that more adequately characterize the assemblages, we find that the observed differences in Whittaker's β from temperate to tropical forests were largely expected given the differences in the species pool. That is, once species pool-related sampling effects were taken into account, there do not appear to be any meaningful differences in the spatial structuring of these two forests.

Discussion and Conclusions

Building on previous work using rarefaction and coverage-based approaches (Chao and Jost 2012, Chao et al. 2014, Chase et al. 2018, McGlinn et al. 2019), we developed a metric standardized by sample coverage to quantify the degree of intraspecific spatial aggregation, independent of changes in the size of the species pool and the regional SAD. Our theoretical considerations and simulations of spatially explicit assemblages show that β_C remains unaffected by changes in the species pool, which allows for comparisons of intraspecific aggregation along large biogeographic gradients. Our empirical case studies suggest that the magnitude of intraspecific aggregation does not change along a latitudinal gradient of forest plots. Importantly, our method requires analysts to determine the target completeness using information contained in the samples from their study. In the case of the commonly used Gentry plots, this shows that the samples cover only a small fraction (10%) of the individuals in the underlying assemblages, and may therefore of limited use for making inferences about their small-scale spatial structure (Tuomisto and Ruokolainen 2012).

Our approach represents an important advance over existing methods to measuring spatial aggregation because of its strong link to existing biodiversity sampling theory. Specifically, we use the γ-scale rarefaction curve as an analytical null model for the expected α-diversity in the absence of spatial structure. While conceptually similar to existing null models, our approach has several advantages. For example, it bypasses the computation of Whitaker's beta and subsequently β-deviation. Instead, we measure the deviation between γ- and α-scales directly from the IBRE curves. β_C can be thought of as the factor by which spatial structure has reduced α diversity compared with the random expectation. This makes it more intuitive than β-deviation (Kraft et al. 2011, Xing and He 2021) because it can be directly interpreted as an effective number of distinct communities (Jost 2007), conditional on the estimated sample coverage. Additionally, our approach explicitly incorporates an estimate of sample completeness into the analytical workflow, which means that the analyst is confronted with the limitations of the data.

Ulrich et al. (2017) have argued that null model approaches are limited in their ability to disentangle species pool and aggregation effects, unless they incorporate external data on the sizes of the relevant species pools. Here, we make use of the idea that the sample itself can also provide an estimate of its completeness (Good 1953, Chao and Jost 2012). Our method uses the shape of the IBRE curve, itself determined by the SAD, to draw inferences for an estimated constant fraction of the individuals in the underlying community (i.e., a constant sample coverage). This approach to standardization implicitly assumes that there is an asymptote in species diversity (Chao and Jost 2012). While this assumption is mathematically convenient, it cannot strictly be true; due to species aggregation at higher scales, we will always find more species with more samples, until the entire global pool is sampled

(Williamson et al. 2001). Nevertheless, β_C does not extend to the asymptote itself, but merely employs a useful approximation of sample completeness via sample coverage. As spatial structure is an inherently scale-dependent phenomenon, with this approach we can only measure it at the spatial grain prescribed by the samples (i.e., spatial structure within the γ-scale). Even when extrapolation is used, the spatial grain of the data remains unchanged. For a scale-dependent examination of spatial aggregation, we recommend comparing results obtained from different spatial grains.

While β_C isolates the degree of spatial aggregation, it does not have some of the properties that are sometimes considered essential for β-diversity metrics (Jost 2007, Tuomisto 2010*a*). For example, traditional β-diversities range between unity and the total number of sampling units, and they can be transformed into N-community (dis)-similarities in the range [0,1] (Jost 2007, Chao and Chiu 2016). In contrast, β_C can only reach the number of samples when the samples have a coverage of 1 (i.e., C_{target} is 100%) (see Appendix S3). In such cases, where the curves have reached an asymptote, β_C equals Whittaker's β and one can derive the corresponding (dis-)similarity. However, for incomplete samples, the *N*-community transformation of β-diversity is generally not recommended (Chao and Chiu 2016), and we consider it a strength of our method that it exposes such situations. Only in the rare cases where C_{target} is 100%, classical β-diversity metrics and pairwise (dis)-similarities will not be affected by the species pool.

Although our approach accounts for differences in sample completeness, it still requires standardized sampling or post hoc standardizations (i.e., rarefying samples to the same number and spatial extent) to make valid inferences. The sampling effects we treat here arise passively due to differences in species pools, and not as a result of different sampling strategies and/or effort. For example, the forest plots in our case studies were completely sampled in the sense that every tree was counted in a given area or subplot. However, with respect to the regional species pool or even just the observed γ diversity, a subplot of a given size in the tropics is likely a much less complete sample, compared to an equally sized subplot a temperate region, even when all individuals are counted in each subplot. It is this interaction of sampling effort and the size of the species pool that leads to the null expectation of increasing sample differentiation with increasing species pool size, and for which our method adjusts.

In conclusion, our approach allows us to explicitly disentangle non-random spatial patterns of species diversity (e.g., intraspecific aggregation) amidst variation in species pool size and associated sampling effects. Together with other diversity metrics sensitive to diversity components such as the SAD and total community abundance (Chase et al. 2018, McGlinn et al. 2019), β_C allows deeper insights into how spatial structuring within communities influences patterns of biodiversity and its change. Applications could, for example, shed light onto the assembly processes that govern (meta-)communities along biogeographic gradients and contribute to a better understanding of the spatial diversity patterns that underlie the scale-dependent biodiversity trends observed during the current biodiversity crisis.

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DATA AVAILABILITY

Code and data (Phillips and Miller 2002, Orwig et al. 2015, Condit et al. 2019) are available from Zenodo: https://doi.org/10.5281/zenodo.4727184.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3745/full

Chapter 3 – How does variation in total and relative abundance contribute to gradients of species diversity?

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RESEARCH ARTICLE

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How does variation in total and relative abundance contribute to gradients of species diversity?

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Abstract

Patterns of biodiversity provide insights into the processes that shape biological communities around the world. Variation in species diversity along biogeographical or ecological gradients, such as latitude or precipitation, can be attributed to variation in different components of biodiversity: changes in the total abundance (i.e., more-individual effects) and changes in the regional species abundance distribution (SAD). Rarefaction curves can provide a tool to partition these sources of variation on diversity, but first must be converted to a common unit of measurement. Here, we partition species diversity gradients into components of the SAD and abundance using the effective number of species (ENS) transformation of the individual-based rarefaction curve. Because the ENS curve is unconstrained by sample size, it can act as a standardized unit of measurement when comparing effect sizes among different components of biodiversity change. We illustrate the utility of the approach using two data sets spanning latitudinal diversity gradients in trees and marine reef fish and find contrasting results. Whereas the diversity gradient of fish was mostly associated with variation in abundance (86%), the tree diversity gradient was mostly associated with variation in the SAD (59%). These results suggest that local fish diversity may be limited by energy through the more-individuals effect, while species pool effects are the larger determinant of tree diversity. We suggest that the framework of the ENS-curve has the potential to quantify the underlying factors influencing most aspects of diversity change.

KEYWORDS

Hill numbers, Hurlbert ENS, latitudinal diversity gradient, more-individuals hypothesis, passive sampling, rarefaction

TAXONOMY CLASSIFICATION

Biodiversity ecology; Biogeography; Community ecology

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1 | INTRODUCTION

A fundamental question in ecology is to understand how and why local biodiversity changes from place to place and time to time (Gaston, 2000; Rosenzweig, 1995). Diversity gradients can arise from a number of natural and anthropogenic drivers, and they can inform ecological theory and biodiversity conservation. For example, species richness (i.e., the number of species in a sample) varies along ecological gradients of productivity (Currie, 1991; Mittelbach et al., 2001) and disturbance (Connell, 1978; Miller et al., 2011; Randall Hughes et al., 2007) and along geographic gradients, such as latitude (Fine, 2015; Willig et al., 2003), elevation (Rahbek, 1995), and island size (Kreft et al., 2008). The quantification of diversity gradients from ecological samples is not a trivial problem because diversity is an inherently multidimensional and scale-dependent quantity that encompasses the occurrences and abundances of multiple species simultaneously and changes with sample size, effort, and spatial scale (Chase et al., 2018). Therefore, species richness usually does not sufficiently capture the nuance underlying any pattern of species diversity.

While the exact drivers and processes shaping diversity gradients are manifold, all of them generally invoke responses in at least one of three broad components of species diversity (Chase & Knight, 2013; He & Legendre, 2002; McGill, 2011): (1) the species abundance distribution (SAD) of a regional species pool (i.e., the total number of species in a region and their relative and absolute frequencies), (2) the total abundance (i.e., the number of individuals [*N*] supported by the environment), and (3) the spatial distribution of species in the region (e.g. intraspecific aggregation and interspecific associations). The interplay of these mutually dependent components determines the shape of the regional species–area relationship and ultimately the diversity of local samples at any spatial scale (Tjørve et al., 2008). Therefore, analyzing diversity in terms of these components can provide deeper insights into the nature of multidimensional biodiversity patterns than analyses of species richness alone (Blowes et al., 2017; Chase et al., 2018), and in turn, this may allow for a better understanding of the processes that shape and maintain diversity gradients at a given scale (Blowes et al., 2020; Gooriah et al., 2021).

For example, a classic hypothesis links species richness gradients to variation in total community abundance, which itself can result from resource and energy gradients, differences in available area or anthropogenic factors (Brown, 2014; Srivastava & Lawton, 1998; Storch et al., 2018; Wright, 1983). The most basic version of this more-individual hypothesis describes a passive sampling effect, whereby communities with high total abundance simply randomly capture a higher portion the regional species pool than communities with low abundance (Coleman et al., 1982). Such a scenario is qualitatively different from a situation where instead of total community abundance, the SAD of the regional species pool changes along the observed diversity gradient. The evenness and size of the species pool can vary due to various natural and anthropogenic factors that affect species occurrences and abundances in a species-specific manner, for example, biotic interactions such as competition and predation (Paine, 1974), variation in resource and habitat diversity (MacArthur, 1965; Tilman, 1982), and species specific responses to environmental and anthropogenic filters (Blowes et al., 2020).

To disentangle the components underlying diversity patterns (e.g., SAD and total abundance), it is generally advised to consider several metrics of biodiversity simultaneously because different incidence and abundance-based diversity metrics (e.g., Hill Numbers, rarefied richness, evenness, and beta-diversity) capture the aspects of multidimensional diversity change in a complementary manner (Chao et al., 2014; Chase et al., 2018; McGlinn et al., 2019; Roswell et al., 2021). For example, by comparing patterns in observed species richness to those in rarefied richness (i.e., richness standardized for abundances), it is possible to assess whether a diversity gradient is accompanied by more-individuals effects or changes in the regional species pool (Chase et al., 2018). However, such approaches typically only offer qualitative insights because effect sizes from different diversity metrics are not quantitatively comparable (Dauby & Hardy, 2012). For example, one may find that more-individual effects seem to play a role for a gradient, but it usually remains unclear exactly what proportion of a diversity gradient can be attributed to variation in total abundance and associated passive sampling effects, and what percentage to changes in the regional SAD (but see McGlinn et al., 2019, 2021).

Here, we present a quantitative dissection of the relative importance of changes in *N* versus changes in the SAD for driving patterns of local species diversity. Effects of aggregation only emerge at larger spatial scales and require spatially explicit data, and we do not address aggregation further here. For our approach, we decompose the total diversity of a sample into two additive components. One component is driven by the SAD and its changes, and the other is driven by the number of individuals (*N*) and associated passive sampling effects. The SAD-component can be thought of as the sample's expected diversity for a standard number of individuals (*n*), and the *N*-component is the portion of the observed diversity that is attributable to the fact that a sample exceeds this standard number of individuals (i.e., *N*-component = total diversity – SAD-component). Then, we can analyze and compare the changes in the two components (which we call SAD-effects and *N*-effects), rather than simply analyzing the total diversity change. To calculate the components, we use the effective numbers of species (ENS) transformation of the rarefaction curve (Dauby & Hardy, 2012), which allows us to express SAD- and *N*-components in the same units of ENS. We illustrate our approach by applying it to two empirical data sets that have strong latitudinal gradients of local species richness (i.e., reef fishes and trees) and show that they emerge from different relative contributions of changes in the regional SAD and in the number of individuals.

2 | ENS RAREFACTION AND RELATED APPROACHES

Our approach relies on a family of diversity measures that was first introduced as “Hurlbert ENS” by Dauby and Hardy (2012). Here, we use the term “ENS rarefaction” to emphasize that these measures are simply an effective number of species (ENS) transformation of the individual-based rarefaction (IBR) curve (Hurlbert, 1971). Since ENS rarefaction is one of the lesser-known, but quite powerful, families of diversity measures, we briefly explain it below and compare it with the related Hill number framework, and the IBR framework that it is based on (see Table 1).

Relating the complementary information given by a set of diversity measures to the diversity components discussed above is challenging because many metrics are sensitive to more than one component (Chase & Knight, 2013). Furthermore, diversity metrics often differ in their numerical ranges and units (i.e., their numerical constraints), and in the degree to which they are affected by passive sampling effects, which in statistics is called estimation bias (Gotelli & Chao, 2013). For example, species richness, which counts all species independent of their abundance, can attain any integer number, and is strongly affected by the number of individuals in the sample. In contrast, Simpson's index, which gives disproportionately high weight to the dominant species of the SAD, ranges between 0 and 1 and is almost unaffected by sample size (i.e., the number of individuals). Although the two metrics hold complementary information on the SAD and passive sampling effects, their different numerical constraints and estimation biases make it difficult to disentangle the two components and compare their effect sizes (Jost, 2006).

The Hill number framework solves the problem of incompatible numerical constraints by converting diversity index values to effective numbers of species (Equation 1 in Table 1). This encompasses all diversity indices that are a function of the term $\sum_{i=1}^{S} p_i{}^q$(e.g., species richness for q = 0, Shannon index for q = 1 and Simpson's index for q = 2), where the diversity order, q, tunes the weight of species abundances p_i (Hill, 1973; Jost, 2006; Rényi, 1961). The term ENS refers to the hypothetical number of species that a perfectly even sample would have if it produced the same index value as the real sample. Hence, Hill numbers relieve diversity indices of their numerical constraints by re-expressing them in units equivalent to that of species richness (Jost, 2006). However, like most diversity metrics, Hill numbers retain a downward estimation bias, whose strength diminishes with increasing values of the diversity order q (Chao et al., 2014). Therefore, differences in Hill number profiles cannot unambiguously be attributed to changes in the regional SAD or changes in total abundance. For example, if ${}^2D$ (corresponding to Simpson's index) is constant along a gradient of interest while ${}^0D$ (i.e., species richness) increases, this pattern can be underlain by a change in the regional SAD (i.e., an increase in the number of rare species), a passive sampling effect (i.e., an increase in total abundance) or both.

IBR is a framework that explicitly addresses passive sampling effects by expressing diversity in terms of the expected number

TABLE 1 Comparing Hill numbers, individual-based rarefaction, and ENS rarefaction frameworks for quantifying diversity

	Hill numbers	Individual-based rarefaction	ENS rarefaction
Symbol	${}^qD$	S_n	E_n
Formula	${}^qD = \left(\sum_{i=1}^{S} p_i^q\right)^{\frac{1}{1-q}}$ Equation (1)	$S_n = S - \sum_{X_i \geq 1} \frac{\binom{N-X_i}{n}}{\binom{N}{n}}$ Equation (2)	$S_n = E_n\left(1 - \left(1 - \frac{1}{E_n}\right)^n\right)$ Equation (3)
Range	1, N	1, n	1, ∞
ENS	Yes	No	Yes
Estimation bias	Downward bias for $q < 2$	Unbiased	Unbiased
Description	ENS transformation ("true diversity") of any diversity index that is a function of $\sum_{i=1}^{S} p_i^q$ (e.g. Richness ($q = 0$), Shannon ($q = 1$), Simpson ($q = 2$)); Defined as the species richness of a hypothetical perfectly even community that has the same diversity index value as the sample	The expected species richness of a sample of n individuals ($n < N$)	ENS transformation of S_n. Defined as the species richness of a hypothetical community that has the same rarefied richness (S_n) as the sample and infinitely many individuals
Influence of relative abundances	The higher q, the lower the influence of rare species	The higher n, the higher the influence of rare species	The higher n, the higher the influence of rare species
References	Hill (1973), Jost (2006)	Hurlbert (1971), Gotelli and Colwell (2001)	Dauby and Hardy (2012)

Note: S, observed species richness; p_i, relative abundance of species i; q, exponent that determines the sensitivity to rare species (0 = very sensitive, 2 = not very sensitive); N, observed number of individuals in the sample; X_i number of individuals of species i; ENS, the effective number of species which is the number of equally abundant species that results in the same value of diversity as the sample. To calculate E_n, Equation 3 can be solved numerically for given values of S_n and n.

of species for a standardized number of individuals (Equation 2 in Table 1) (Gotelli & Colwell, 2001; Hurlbert, 1971). The resulting non-linear scaling relationship between the number of individuals (n) and expected species richness (i.e., rarefied richness, S_n) is the IBR curve (Figure 1). Rarefied richness estimates are unbiased for random samples, which means that they only respond to changes in the SAD but not to the original number of individuals present in the sample N. By varying the reference sample size n, IBR can give more or less influence to species abundances (Gotelli & Colwell, 2001). However, the value of n also constrains the numerical range of rarefied richness values. Thus, effect sizes at the base of the IBR curve (representing mostly common species) are not directly comparable to those at higher values of n (representing both common and rare species; Dauby & Hardy, 2012). In other words, if we find a species richness gradient to be steeper than a corresponding gradient in rarefied richness, part of the numerical difference has nothing to do with more-individual effects, but is merely the null expectation from the different numerical constraints of the two metrics.

ENS rarefaction is method that converts the IBR curve into effective numbers of species with consistent numerical constraints along the curve (Figure 1). There is no simple closed-form equation for ENS rarefaction but Dauby and Hardy (2012) showed that numerical approximation of Equation 3 in Table 1 can be used to convert any S_n value to its corresponding effective number (E_n). Again, ENS refers to the number of species in a hypothetical, perfectly even community that has the same rarefied richness as the real community (Dauby & Hardy, 2012). The base of the resulting “ENS curve” (i.e., E_2) is also the ENS transformation of Hurlbert's (1971) unbiased probability of interspecific encounter (S_{PIE}, Olszewski, 2004), and is equal to an asymptotic estimate of the Hill number ^2D (Chao et al., 2014; Dauby & Hardy, 2012). It can be interpreted as the number of dominant species in the species pool because being at the base of the curve it gives disproportionately high weight to species with high relative abundances. As n increases along the ENS curve, rarer and rarer species influence the diversity estimate until it practically converges onto the observed total species richness, where all species are counted regardless of their abundance (i.e., E_N). Increases along the ENS curve are entirely due to the incremental influence of rare species and do not result from variable numerical constraints along the curve. Therefore, the ENS transformation makes it easy to assess relative evenness; random samples from perfectly even communities (i.e., communities without rare species) produce ENS curves that are flat horizontal lines (Dauby & Hardy, 2012). In some sense, ENS rarefaction combines the advantages of Hill numbers and IBR in a single family of diversity measures. It has unconstrained values for all values of n and, being a simple transformation of rarefied richness, its values for a reference sample size n are only affected by the SAD and not by the actual number of individuals captured in the sample. Therefore, differences in E_n values for a constant n can be unambiguously attributed to changes in the SAD, while comparisons between different levels of n reflect a quantification of the more-individuals effect. These properties make ENS rarefaction a useful tool for the decomposition approach we present here.

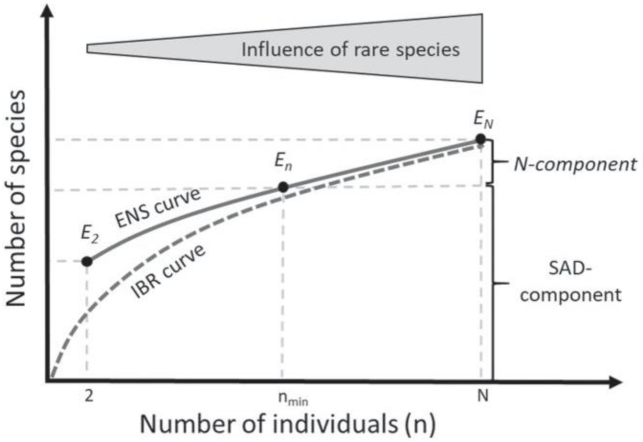

FIGURE 1 Schematic drawing of an individual-based rarefaction (IBR) curve and the corresponding effective number of species (ENS) curve. The IBR curve is constrained by the values of n (i.e. it is bound to start at the $x = y = 1$), whereas the ENS curve is unconstrained on the vertical axis. The ENS value for a standardized number of individuals E_n reflects the “SAD-component” in our framework. The difference between the total diversity (ENS_N) and the SAD-component (ENS_n) results from the fact that samples usually exceed the number of individuals n_{min} used for standardization. As this portion of the total diversity change reflects abundance variation, we call it “N-component”.

3 | ANALYTICAL FRAMEWORK

Figure 2 illustrates how we use ENS rarefaction to disentangle the diversity components in practice. For this purpose, imagine a latitudinal diversity gradient between a temperate (low diversity) community and a tropical (high diversity) community. We consider three scenarios of how this diversity gradient can manifest in terms of SAD and N variation. First, a more-individuals effect (panels a, d, and g); second, a change in the regional SAD (panels b, e, h); and third, a combination of more-individuals effect and SAD change (panels c, f and i). The first row of Figure 2 (panels a, b, c) shows the IBR curves corresponding to the 3 scenarios. Panel a depicts the more-individuals effect, where the tropical community (green) has twice as many individuals as the temperate one (yellow) and therefore samples a larger fraction of its species pool. However, when standardized to a common number of individuals, both communities are expected to yield the same diversity (i.e., the IBR curves follow the same trajectory), which reflects that they are samples from similar regional SADs. Compare that with panel b, where the number of individuals is the same for both communities, but their SADs differ (i.e., the IBR curves have different shapes). In this scenario, the tropical community samples from a larger species pool with a higher number of relatively common species and many more relatively rare species, which results in an IBR curve that is steeper than the temperate one. Finally, panel c represents a scenario where the diversity gradient is underlain by a combination of more-individuals effects and SAD changes. Not only does the tropical community sample a more diverse SAD but also it harbors a larger number of individuals.

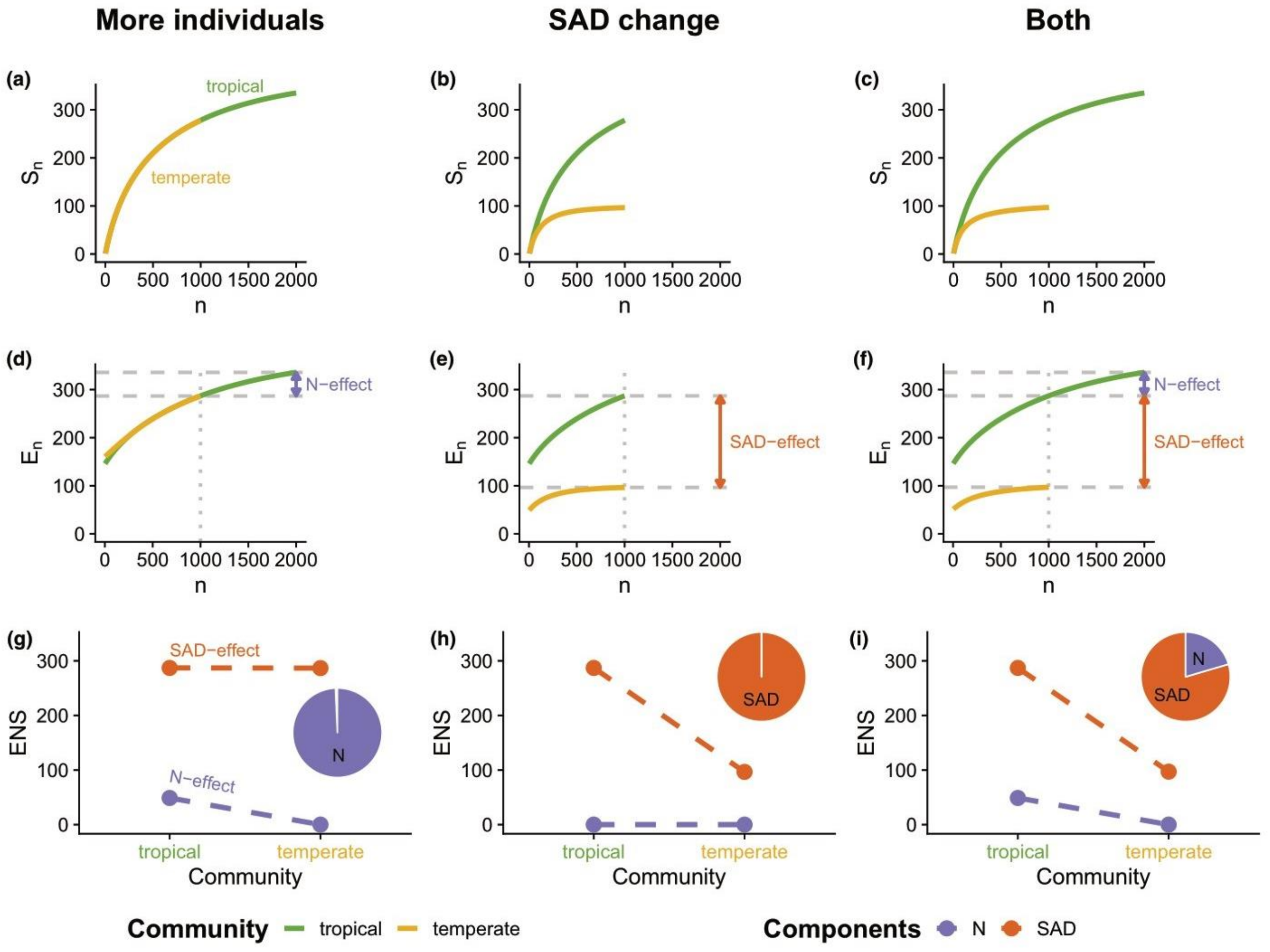

FIGURE 2 Schematic overview of the analytical framework. Using individual-based rarefaction curves (a–c) and their conversion to effective numbers of species (ENS) (d–f), diversity change can be dissected into contributions of SAD effects and *N* effects. The columns represent 3 hypothetical scenarios of diversity patterns between a diverse "tropical" and a less diverse "temperate" local community. In first scenario (a, d, g), the difference in diversity results from a passive sampling effect, as the tropical community supports more individuals than the temperate one. In the second scenario (b, e, h), abundance remains constant, but the pattern is underlain by differences in the regional species abundance distribution (SAD, i.e. larger species pool in the tropics). In the third scenario (c, f, i), both abundance and the regional SAD vary between the two communities. Using the ENS conversion, the total diversity of each sample is dissected into a SAD-component and an *N*-component (dots in g–i). By examining the difference of the components between the communities, we can quantify the corresponding SAD effects and *N* effects (pie charts in g–i).

While the IBR curves allow us to qualitatively and visually distinguish the scenarios, they do not directly enable a quantitative decomposition of the observed diversity change into contributions of more-individuals effects and SAD. Therefore, we apply the ENS transformation to free IBR curves of their numerical constraints. The resulting ENS curves (second row) are similar to the IBR curves in that changes in their shape reflect changes in the SAD, but the start of the curve is no longer constrained. In the more-individuals scenario (panel d), both communities have the same diversity for any common number of individuals (up to $n = 1000$). Beyond that, the tropical community passively samples additional rare species due its larger sample size (labeled as "*N*-effect"). In the SAD change scenario (panel e), the ENS transformation reveals that the tropical community has a higher number of relatively dominant species to start with (i.e. E_2), and then accumulates relatively rare species at a higher rate than the temperate community, adding up to the total SADeffect (labeled "SAD-effect"). The same SAD-effect can be observed in the combined scenario (panel f), but now the tropical community also has additional rare species due to its higher number of individuals (labeled "*N*-effect"). As along the ENS curve all values are expressed in terms of effective numbers of species, we can directly compare the magnitudes of the two effects. In this example (panel f), most of the observed diversity change is attributed to changes in the regional SAD (ca. 80%), while the contributions of the more-individual effect are relatively small (ca. 20%).

To apply this approach to any number of communities, we can partition the total diversity of each community (i.e. E_N) into two components: The SAD-component is simply the ENS for a standard number of individuals (i.e. E_n), where n is typically the sample size of the smallest community in the gradient. Then, the N-component is the difference between the total diversity and the SAD-component (i.e. $E_N - E_n$). It reflects the more-individuals effect with respect to n individuals (i.e. how much more diversity does a community have because its sample size exceeds n). Now, instead of considering the total diversity (E_N), we can analyze these components along the gradient of interest. This is shown in the last row of Figure 2, where the orange and purple dots represent the SAD- and N-components of the two example communities. Note that adding up the two components yields the total diversity of the communities. In the first scenario, the diversity change occurs exclusively in the N-component (i.e., a N-effect), while in the second scenario, the diversity change is driven by the SAD-component (i.e., a SAD-effect). Finally, in the third scenario both components change at the same time, so that N effect and SAD effect add up to the total diversity gradient. By comparing the slopes of the two components along the gradient (dashed lines), we can assess the relative contributions of N effects and SAD effects to the observed diversity gradient. The pie charts in Figure 2 illustrate the contributions of SAD effects and N effects for each scenario. In the combined scenario (panel i), the SAD effect contributes 80% toward the total diversity gradient while 20% of the diversity change occurs because the tropical community has more than 1000 individuals. In practice, these effect sizes correspond to the regression coefficients of linear models. However, the components could also be modeled as non-linear functions of continuous predictors. In that case, the contributions of N and SAD effects may be variable along the gradient and cannot be summarized as a simple pie chart.

4 | SIMULATION

To quantitatively examine the behavior of the two components with respect to variation in the SAD and total abundance, we carried out a simulation study using the R package mobsim (May et al., 2018). We simulated spatially explicit Poisson communities (i.e., species had random spatial distributions) with different SADs and total abundances. We assumed lognormal SADs for the simulated communities and parameterized them with different species pools (100, 200, 300, 400, 500 and 600 species) and total abundances (1000, 2000, 3000, 4000, 5000, and 6000 individuals) in a full-factorial design, using 20 replicates for each factor combination. We then sampled each of the communities with a constant quadrat size corresponding to 20 percent of the total area. Following the approach outlined above, we calculated the SAD- and N-components for the samples and examined how they responded to the simulation parameters (i.e., species pool and total abundance). Our simulations show that the SAD-component responded to changes in the species pool but remained unaffected by total abundance (Figure S1). Conversely, the N-component consistently responded to changes in total abundance and was unaffected by changes in underlying SAD (Figure S2). The findings from these simulations are consistent our theoretical expectations from the IBR curve, and the conceptual example is shown in Figure 2.

5 | CASE STUDIES: CONTRASTING LATITUDINAL GRADIENTS IN TREES AND REEF FISH

We used our approach to analyze two empirical datasets documenting latitudinal diversity gradients (LDG) in reef fish and trees. The trend of increasing diversity from poles to equator is one of most prominent global biodiversity patterns that occurs in many taxa and at different spatial scales (Fine, 2015; Hillebrand, 2004; Willig et al., 2003). All components, particularly N and the SAD, likely vary along the gradient, though how they combine to form the LDG at a given scale, and whether this varies among taxa, is less well known.

For example, N is expected to vary with energy- or resource availability and, accordingly, the more-individual hypothesis (MIH) is one of the classic explanations for the LDG (Brown, 2014; Srivastava & Lawton, 1998; Wright, 1983). Historically, the MIH has referred to a collection of different mechanisms by which higher total abundance translates to higher species diversity, including effects on extinction and speciation rates (Evans et al., 2005; Scheiner & Willig, 2005; Storch et al., 2018). However, here we use the term more narrowly to only mean passive sampling effects (Coleman et al., 1982), which is the process by which larger communities (e.g. in the tropics) randomly sample a larger portion of a species pool than small ones (e.g. in temperate regions) (Wright, 1983). Abundance-related processes that influence extinction (e.g. demographic stochasticity) and diversification rates over the longer term likely alter the SAD and regional species pool, and therefore would be captured by SAD effects in our framework. Indeed, there are a large number of ecological and evolutionary mechanisms that shape and maintain latitudinal gradients in regional SADs. These include differences in time for speciation, environmental stability, species interactions, and niche-processes (Fine, 2015). While the LDG is generally strongest at larger spatial grains (Hillebrand, 2004), it is largely unknown how such species pool gradients combine with gradients of total abundance to determine local-scale diversity gradients.

Here, we applied the analytical framework to analyze latitudinal gradients of two publicly available datasets with standardized community surveys: (1) forest trees from the Gentry plot dataset (Gentry, 1988, Phillips & Miller, 2002) and (2) reef fish from the Reef Life Survey (Edgar et al., 2020; Edgar & Stuart-Smith, 2014). Importantly, both data sets use a fixed sampling effort in terms of plot/transect size for their respective sites. Therefore, latitudinal variation in sample diversity reflects changes in the regional species pool (SAD) as well as natural variation in the observed number of individuals (i.e. more-individuals effect).

Because our main focus was to illustrate the analytical framework, rather than an exhaustive analysis of these data sets, we reduced both data sets into one latitudinal "slice" to minimize other well-known confounds, such as biogeographic factors, that influence the magnitude of the gradient. For trees, we focused on the plots located in the Americas, so as to avoid the potential influence of continent on tree diversity (Qian & Ricklefs, 2000). And for the reef fish, we only included surveys from the Indo-Pacific area where diversity is highest, and biogeographic effects (e.g., distance from diversity center) were minimized (Blowes et al., 2017). For both data sets, we excluded sites with fewer than 20 individuals (we also used different cutoff-levels to test the robustness of our results). Figure S3 shows the geographical location of samples included in our analyses.

After selecting the sites, we dissected the observed diversity of each sample into the SAD-component and the *N*-component, assuming a reference sample size of $n = 20$. To do this, we calculated the observed richness and the rarefied richness (S_n) for $n = 20$ and derived the corresponding ENS values using Equation 3 in Table 1 (i.e. E_N and E_n, respectively). E_n represents the SAD-component. The difference between E_N (total diversity) and E_n (SAD-component) is the diversity component that results from the changes in *N* or the more-individuals effect (*N*-component). We then modeled the two components along the latitudinal gradient using simple linear models with absolute latitude as the independent variable, and the SAD and *N*-components as dependent variables. We used the regression coefficients (or slopes) as the effect sizes for the respective components. Since our partitioning framework is additive and models are linear, the effect sizes (i.e. slopes) of the two components add up to the effect size (i.e. slope) of the total diversity gradient.

Both trees and reef fish showed similar slopes along their respective latitudinal gradient for the overall richness gradient, but they differed in how the underlying component contributions changed along the gradient (Figure 3). The trees had a relatively large SAD effect; that is, even when the number of individuals was standardized, the diversity gradient remained quite strong. This suggests that the diversity gradient is mostly underlain by changes in the species pool and associated patterns of commonness and rarity (i.e., the SAD). Nonetheless, the *N*-effect also contributed to the total diversity gradient, as total tree abundance tended to increase as absolute latitude decreased. In contrast to the trees, the reef fish diversity gradient was strongly dominated by the *N*-effect. For a standardized number of individuals, the fish diversity gradient was relatively weak (see SAD-component). This reflects that species rich reef fish communities are often dominated by a few species, the number of which does not vary strongly along the gradient. For a constant sample size, the many rare species in diverse fish communities have little weight in the diversity estimate. That is, they mostly affect the diversity for communities with more individuals and are captured more-individual effect.

The contrasting results between fishes and trees could reflect biological differences of the two groups. Fish move in a three-dimensional space, which allows for much stronger gradients in total abundance. In forests, on the other hand, stem density is likely more strongly limited by available space. This suggests that for forests, community assembly processes change more strongly along the gradient, leading to communities with high relative evenness in the tropics (Ulrich et al., 2016). This is reflected in the strong SAD-effect.

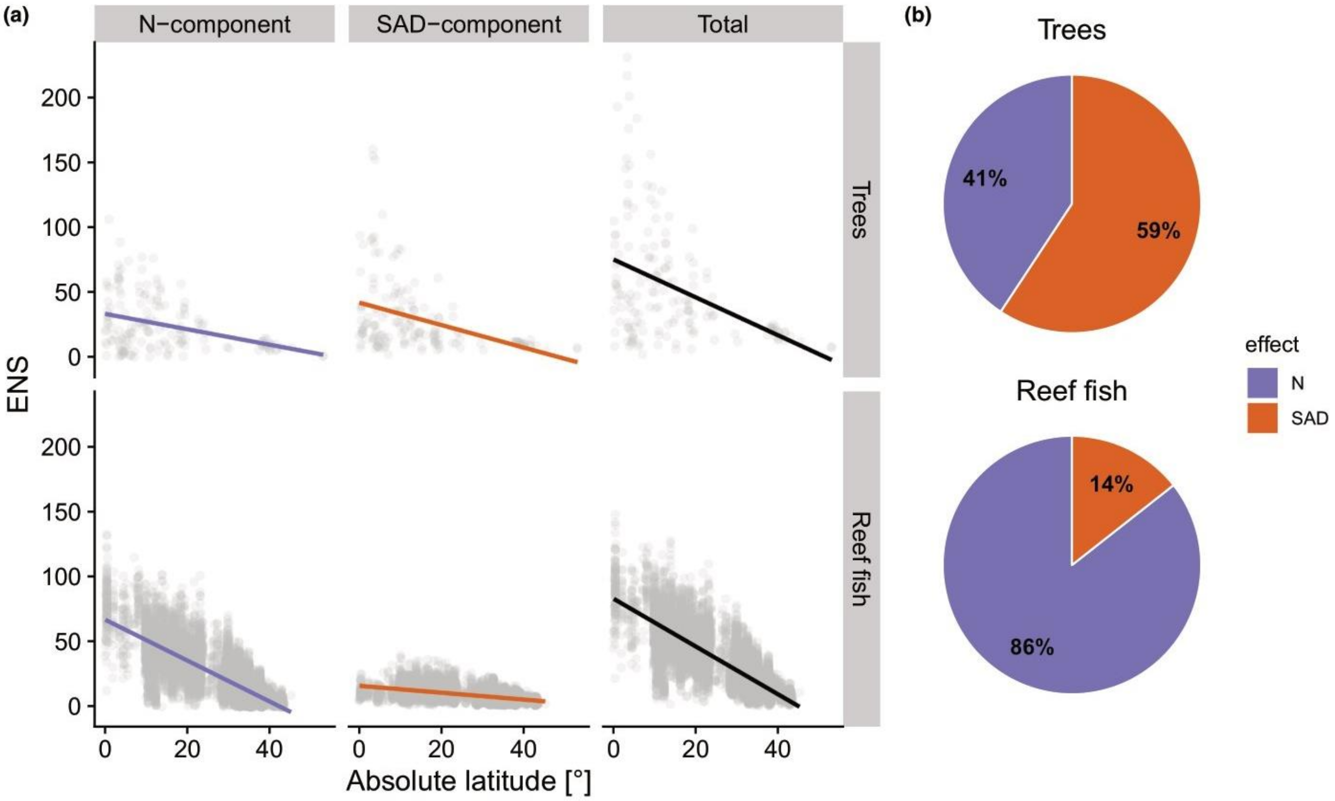

FIGURE 3 Latitudinal diversity gradients of trees and reef fish. (a) *N*-component, SAD-component, and total diversity. Lines represent linear model fits. (b) Relative contributions of *N*-effects and SAD-effects toward total diversity gradient, quantified as the corresponding slopes in (a).

Conversely, the schooling nature of some tropical fishes allows for the dominance of a few species. Additionally, the number of dominant fish species does not vary strongly along the gradient, whereas the number of rare species (which are affected by sampling effects) does. Hence, we find the large *N*-effect in fishes.

6 | DISCUSSION

In this paper, we have outlined a quantitative approach for decomposing local diversity change into contributions of changing SADs and more-individual effects. Using two latitudinal gradients that have similar patterns of species richness, but very different kinds of diversity change, we illustrated the utility of this approach. For trees, a major part of the gradient was attributable to changes in the dominant part of the SAD (59%). Whereas, for reef fishes the diversity gradient was mostly underlain by more-individual effects (86%). Our case study shows that our approach has great potential for quantitative synthesis studies that analyze the heterogeneity in seemingly general diversity patterns (such as the LDG).

It is not a new idea to describe the diversity components using different metrics derived from the IBR curve (e.g. S_{PIE}, S_n, S, N) (Chase et al., 2018; Hurlbert, 1971; McGlinn et al., 2019; Olszewski, 2004). However, it has been difficult to quantitatively combine the lines of evidence described by multiple metrics, as the corresponding effect sizes are usually not directly comparable. The novelty of our approach is that it uses the common currency of effective numbers of species to decompose the diversity of a sample into a SAD-component and a *N*-component that are directly comparable. Whilst deriving our approach, we also shed light onto the commonly overlooked diversity framework of ENS rarefaction (Dauby & Hardy, 2012), pointing out its great utility by comparing it to Hill numbers and IBR. Importantly, however, we do not want to imply that ENS rarefaction is always preferable to the other two families of diversity measures. As a matter of fact, all three families are perfectly suitable representations of a given SAD that carry the same information and allow for conversion between them (Chao et al., 2014; Dauby & Hardy, 2012).

Although we decompose the observed diversity into distinct components, it is important to realize that the components do not strictly exist or change in isolation from another. For example, more-individual effects can only occur in the presence of a larger scale SAD, and conversely, no species pool can be maintained without the individuals that populate it. Furthermore, the components do not *cause* the observed species richness but rather they concomitantly go along with it. Despite this mutual dependence, we think that a quantitative dissection is useful from an analytical point of view, and our approach represents a consistent quantitative framework for the description of multidimensional and scale-dependent diversity patterns. Moreover, although our approach is agnostic about mechanism per se, it can provide the empirical patterns to test causal hypotheses of biodiversity variation.

Our approach is applicable for data sets that contain community composition with species abundances that were obtained using standardized sampling procedures. Specifically, we require individual counts and therefore the method is not applicable to indirect proxies of abundance such as biomass or percent cover. If sampling effort varies from sample to sample, the *N*-effect does not only reflect natural variation in community abundance but also the variable sampling effort. Furthermore, like most approaches to measuring diversity, we assume that the samples are random subsets of the species pool (i.e. independence of all individuals in the sample), and that all species have the same detection probability. Whenever these assumptions are violated, sample-based rarefaction approaches may be more appropriate (e.g Gotelli & Colwell, 2001; McGlinn et al., 2019).

Here, we modeled the components of diversity as a linear function with latitude. However, the method can be used to explore more complex, nonlinear functional forms. For example, it may be possible that a linear gradient at the species richness level is actually the compound result of nonlinear underlying components, or vice versa. Furthermore, when data are available at multiple spatial grains, this method can be extended to quantify and dissect the effect of spatial aggregation. To do this, we would analyze how the SAD-component changes between a larger and a smaller scale. Since any scale dependence of SADs are caused by nonrandom spatial distributions, SAD effects between scales can be interpreted as an effect of spatial aggregation (Engel et al., 2021; Olszewski, 2004).

In conclusion, we have shown how the ENS transformation of the rarefaction curve can contribute to quantifying the components underlying diversity gradients. Looking ahead, we think that the ENS curve will be a useful tool for the resolution of a number of open questions regarding the complex interactions between aspects of diversity and sampling. Not only can it shed light onto aspects of evenness in the presence of sampling effects, but when applied across spatial scales, it promises comparable insights into the spatial structure of regionally common and rare species. We hope these approaches will pave the way for a deeper understanding of the patterns and potential drivers of biodiversity change along natural and anthropogenic gradients.

AUTHOR CONTRIBUTIONS

Thore Engel: Conceptualization (lead); formal analysis (lead); methodology (lead); visualization (lead); writing – original draft (lead). **Shane A. Blowes:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (equal). **Daniel J. McGlinn:** Conceptualization (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (equal). **Nicholas J. Gotelli:** Conceptualization (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (equal). **Brian J. McGill:** Conceptualization (supporting); methodology (supporting); writing – original draft (supporting); writing – review and editing (equal). **Jonathan M. Chase:** Conceptualization (supporting); formal analysis (supporting); methodology (supporting); supervision (lead); writing – original draft (supporting); writing – review and editing (equal).

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CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in this study are already entirely in the public domain. The Gentry forest plot data set (Gentry, 1988, Phillips & Miller, 2002) is accessible through the Botanical Information and Ecology Network (BIEN, https://bien.nceas.ucsb.edu/bien/). The RLS data set of global reef fish abundance and biomass (Edgar et al., 2020; Edgar & Stuart-Smith, 2014) is accessible through the Australian Ocean Data Network (AODN, https://portal.aodn.org.au/). We also archived the data in Dryad under https://doi.org/10.5061/dryad.rjdfn2zdt.

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SUPPORTING INFORMATION

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

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Chapter 4 – Synthesizing elevational gradients of abundance and diversity

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Synthesizing elevational gradients of abundance and diversity

Abstract

Aim: Elevational diversity gradients are among the most iconic patterns of biodiversity. In the last decades, several studies have reviewed the relationship between altitude and species richness but so far, there has not been a quantitative synthesis using abundance-based measures of diversity. The aim of this synthesis was to model the global relationship and discern the role of abundance for elevational diversity gradients.

Location: 43 elevational gradients on 5 continents

Taxon: Invertebrates, birds, mammals, plants, herpetofauna

Methods: We compiled data on elevational gradients from the literature and synthesized them using approaches based on individual-based rarefaction and hierarchical models. We only included gradients with constant sampling effort for each sample along the gradient. Our database contained 43 gradients from 5 continents.

Results: Overall, our models show overarching declines of diversity with increasing elevation. The global pattern diminished slightly when we controlled for variation in total abundance, but the general shape of the relationship persisted. Abundance also declined slightly towards summits but not as strongly as diversity. The abundance pattern was more heterogeneous between gradients that the diversity pattern.

Main conclusions: Our findings provide no evidence for the generality of a hump-shaped elevational diversity gradient. The predominantly declining species richness patterns are largely underlain by changes in the species abundance distribution, while passive sampling effects associated with abundance variation seem to play a minor role.

Keywords: mountain, richness, elevation, alpine, synthesis, more-individuals, rarefaction

Introduction

Understanding how diversity and abundance of species vary through space and time is one of the fundamental goals of ecology (Gaston, 2000; Rosenzweig, 1995). Mountain regions have been of particular interest for studying diversity patterns because they typically have a lot of environmental heterogeneity and exceptionally high levels of biodiversity within relatively small spatial extents (McCain & Grytnes, 2010; Rahbek, Borregaard, Antonelli, et al., 2019; Rahbek, Borregaard, Colwell, et al., 2019). Accordingly, elevational gradients are often viewed as “natural laboratories” that provide insights into how diversity patterns emerge and how biological communities respond to changes or gradients in environmental conditions (Sanders & Rahbek, 2012; Tito et al., 2020).

The “elevational diversity gradient”, meaning a pattern of declining species richness with increasing altitude, was historically viewed as universal (Brown & Gibson, 1983; MacArthur, 1984), but more recent evidence has shown high variability in this relationship (Guo et al., 2013; McCain, 2009; McCain & Grytnes, 2010; Rahbek, 1995). Although most studies find that species richness declines toward mountain summits, this is often not a monotonic or linear pattern. Rather, many taxa show humped-shaped mid-elevation peaks, low-elevation plateaus, or low-elevation plateaus with mid-elevation-peaks (McCain, 2005, 2009; McCain & Grytnes, 2010; Rahbek, 1995). Furthermore, the relationship often varies within and among taxa, with latitude with the spatial scale on which it was measured (Rahbek, 2004). Along with climate, isolation and geometric constraints (Colwell & Hurtt, 1994; Lomolino, 2001), abundance variation (reflecting gradients in resources, available energy or productivity) is one of most common mechanisms hypothesized to shape elevational gradients of diversity (McCain et al., 2018). Nonetheless, syntheses on the combined elevational gradients of abundance and diversity are currently lacking.

Whether in samples on mountain slopes or elsewhere, species richness and abundance are tightly coupled quantities. Variation in the number of individuals is often invoked as a first-order explanation for diversity patterns, sometimes referred to as passive sampling effect or more-individual hypothesis (Srivastava & Lawton, 1998; Storch et al., 2018; Wright, 1983). Specifically, abundance and species richness form a non-linear scaling relationship resembling a species area curve, whereby samples or assemblages with high abundance passively capture a higher proportion of their regional species pool than assemblages with low abundance (Coleman et al., 1982). Therefore, patterns of species richness can manifest in qualitatively very distinct ways, depending on the concomitant patterns of total and relative abundance (Blowes et al., 2022;

McGlinn et al., 2019). For example, an elevational decrease in species richness may simply follow from an underlying decreasing pattern of total abundance (i.e. passive sampling), which itself may result from resource gradients or other ecological and stochastic factors that influence the total number of individuals found in a sample. On the other hand, if total abundance remains constant along a sample gradient, any variation in species richness likely reflects changes in the underlying species abundance distribution (SAD, e.g. changes in evenness or the size of the regional species pool along an elevational gradient). Beyond simple passive sampling, the more-individual hypothesis posits that persistent abundance gradients also shape species pools in the long term by influencing species extinction probabilities (Storch et al., 2018; Wright, 1983). However, stochastic abundance variation tends to masks this version of the more-individual effect that plays out on larger time scales, making it unrealistic to detect its imprint in standard ecological samples (Vagle & McCain, 2020).

While many studies have synthesized species richness patterns along elevational gradients, few syntheses have incorporated aspects of total and relative species abundances (but see Wang et al. 2017, Supriya et al. 2019). One of the reasons for this may be that many original studies only collect or report occurrence data that simply do not allow for diversity measures beyond species richness. Furthermore, until recently it was rather uncommon to publish the raw data underlying calculations of biodiversity (e.g. site-by-species abundance matrices). Therefore, most of the available syntheses have been restricted to meta-analyses of the reported effect sizes on simple diversity measures (i.e. mostly species richness) and vote-counting approaches for the shape of the pattern (e.g. decreasing vs hump-shaped diversity gradients). Nonetheless, there are a number of original studies available to investigate the combined gradients of abundance and diversity. For example, for an elevational gradient of bats, Coelho *et al.* (2018) found that both species richness and total abundance declined with altitude, which suggests that variation in total abundance may be an important driver of local species richness along this gradient. Other studies have reported discordant elevational gradients of richness and abundance in different taxa and mountains (Brehm et al., 2007; Kumar et al., 2009), which suggests that the SAD and the species pool change along these gradients.

Here, we present a quantitative synthesis of elevational diversity gradients using abundance-based diversity measures. Specifically, we were interested in the role that abundance variation and associated passive sampling effects play for the observed species richness patterns. To do so, we compiled publically available data sets documenting elevational diversity gradients where data on the abundances and relative abundances of species were given from studies with relatively standardized sampling methodology. We then analyzed these data in a synthetic framework using rarefaction-based diversity metrics and hierarchical models.

Materials and Methods

Data compilation

Our main goal was to collate data from as many open-access datasets as we could find that: (1) collected data from a given taxa using standardized sampling methods where both abundances and relative abundances could be extracted; (2) sampled at least 2 elevations along a given elevational gradient (taking care to minimize variation among mountains, aspect, etcetera), where sampling effort across elevations was standardized, or could be standardized (e.g., using rarefaction). Because of the data intensive needs of our work, and because standardized literature searches can notoriously miss a number of relevant data sources, we opted for an 'inclusive' data search strategy, which has served well for similar syntheses with intense data requirements (Chase *et al.*, 2020; van Klink *et al.*, 2020; Gooriah *et al.*, 2021; Petsch *et al.*, 2021). First, we used a standardized search string in Web of Science with Subject= (elevation* OR altitud* OR height*) AND (biodiversity OR diversity

OR richness* OR "number of species" OR "alpha diversity" OR "alpha-diversity" OR "α-diversity" OR "α diversity" OR "beta diversity" OR "beta-diversity" OR "β-diversity" OR "β diversity") AND (species OR plant* OR bird* OR amphibian* OR mammal* OR reptile* OR butterfl*OR ant* OR insect* OR arthropod* OR beetle* OR moth* OR tree* OR shrub* OR bat*). We explicitly did not include studies on microbes or fungi, or those with percent cover data (e.g., many vegetation datasets) which are not appropriate for our rarefaction-based analyses. While this search yielded more than 1000 potentially useful papers, we were only able to find nine that had provided suitable data for our needs. So we extended our search to be more inclusive, using combinations of the above search terms in Web of Science and Google Scholar. We also scanned the reference lists of some of the available meta-analyses on elevational gradients (e.g. McCain, 2005, 2009; Guo *et al.*, 2013) and did a forward literature search on each of these to see which papers had cited them. Other datasets were referred to us by colleagues or were known to us previously. We obtained the data from tables, supplementary files and linked online repositories. Our final dataset comprised 43 elevational gradients from 39 studies. The majority of studies document invertebrate taxa, but we also were able to analyze some datasets on vertebrate taxa and plants (table 1). The geographical distribution of the data covered most continents (except Australia and Antarctica) and spanned a latitudinal gradient from -25.6ºS to 45.7ºN (Fig 1). The datasets had elevational ranges between 138 and 3750 meters, with a median elevational range of 1688. The number of sites per gradient varied from 2 to 120. For our analysis, we excluded all samples with fewer than 5 individuals.

Table 1: Datasets included in the analysis.

Reference	**Country**	**Broader taxonomic group**	**Narrower taxonomic group**
(Acharya & Vijayan, 2015)	India	invertebrates	lepidoptera
(Bharti et al., 2013)	India	invertebrates	ants
(Brehm et al., 2016)	Ecuador	invertebrates	lepidoptera
(Chen et al., 2020)	China	mammals	nonvolant small mammals
(Choi & An, 2010)	South Korea	invertebrates	lepidoptera
(Choi et al., 2017)	South Korea	invertebrates	lepidoptera
(Choi & Thein, 2018)	South Korea	invertebrates	coleoptera and lepidoptera
(Coelho et al., 2018)	Brazil	mammals	chiroptera
(Eisen et al., 2008)	USA	invertebrates	mosquitos
(Foord et al., 2015)	South Africa	invertebrates	arachnids
(Dianzinga et al., 2020)	France (Reunion Island)	invertebrates	thysanoptera
(García-Gómez et al., 2009)	Mexico	invertebrates	collembola
(Garciano et al., 2014)	Philippines	invertebrates	arachnids
(Gómez-Anaya et al., 2010)	Mexico	invertebrates	odonata
(González-Megías et al., 2008)	Spain	invertebrates	coleoptera
(Monge González et al., 2021)	Mexico	plants	trees
(Highland et al., 2013)	USA	invertebrates	lepidoptera
(Inoue et al., 2006)	Thailand	invertebrates	termites

(Joshi & Arya, 2007)	India	invertebrates	lepidoptera
(Jung et al., 2012)	South Korea	invertebrates	coleoptera
(Kamimura et al., 2017)	Brazil	plants	trees
(Lazzarotto & Lázzari, 1998)	Brazil	invertebrates	aphids
(Maveety et al., 2013)	Peru	invertebrates	coleoptera
(Mbenoun Masse & Makon, 2019)	Cameroon	invertebrates	myriapods
(Musthafa & Abdullah, 2019)	Malaysia	invertebrates	coleoptera
(Nor, 2001)	Malaysia	mammals	nonvolant small mammals
(Nunes et al., 2016)	Brazil	invertebrates	coleoptera
(Palin et al., 2011)	Peru	invertebrates	termites
(Rana et al., 2019)	India	plants	trees
(Ribeiro et al., 2019)	Brazil	invertebrates	wasps
(Sabu et al., 2008)	India	invertebrates	ants
(Sanders et al., 2020)	USA	invertebrates	ants
(Sirin et al., 2010)	Turkey	invertebrates	orthoptera
(Stanbrook et al., 2021)	Kenya	invertebrates	coleoptera
(Sublett et al., 2019)	Peru	invertebrates	lepidoptera
(Wachter et al., 1998)	USA	invertebrates	orthoptera
(Wen et al., 2018)	China	mammals	nonvolant small mammals
(Wiafe & Agyei, 2013)	Ghana	herpetofauna	amphibians
(Zhang et al., 2020)	China	birds	breeding birds

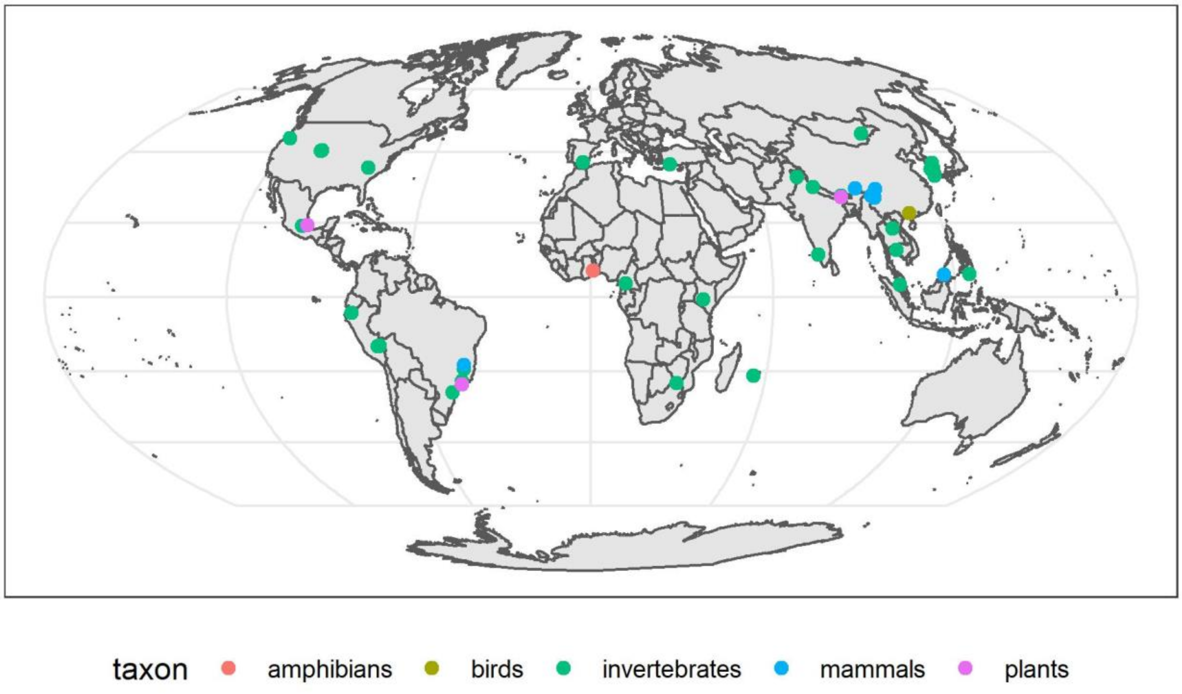

Figure 1: Approximate locations of the gradients included in this study. Colour represents different taxonomic groups.

Quantification of species diversity

As we had abundance data for each species in each sample from the original studies, we were able to calculate the same standardized set of diversity metrics for the samples from all gradients. To quantify diversity, we calculated several metrics that represented different points on the individual-based rarefaction (IBR) curve (Gotelli & Colwell, 2001; Hurlbert, 1971). The IBR curve describes the non-linear relationship between the number of individuals of a sample (n) and the corresponding expected species richness (i.e. rarefied richness, S_n). By examining and comparing different points on the IBR curve, one can discern the role of abundance variation for diversity patterns (Chase et al., 2018; McGlinn et al., 2019; Olszewski, 2004). Here, we used three different points: First, observed species richness (S), which is the total number of species of a sample and corresponds to the endpoint of the IBR curve, where n is equal to the observed number of individuals, N. Second, rarefied richness (S_n) for a constant number of n individuals. For this comparison, we set n to be the smallest number of individuals observed within a given gradient (n_{min}). Third, rarefied richness for n=2 individuals (S_2), which is closely related to the probability of interspecific encounter (PIE) and Simpson's diversity metric (Hurlbert, 1971), and corresponds to the slope at the base of the IBR curve (Olszewski, 2004). These three measures vary in the degree to which they are affected by patterns of commonness and rarity; while species richness counts all species without respect to their abundance, S_n and S_2 are increasingly more sensitive to the evenness of species in the sample. The lower the value of n, the lesser the influence of rare species.

For a better quantitative comparison of the three metrics, we transformed them into effective numbers of species (ENS) following the approach suggested by Dauby and Hardy (2012) and recently described by Engel et al. (2022). Essentially, this step removes the different numerical constraints of the three metrics and, as a result, they can be plotted on the same axis (supplementary figure S1). To go from S_n to the corresponding effective number E_n, we solved the following equation, using numerical approximation (Dauby & Hardy, 2012):

$$S_n = E_n\left(1-\left(1-\frac{1}{E_n}\right)^n\right) \qquad \textit{[Eq. 1]}$$

This resulted in the metrics E_2 (corresponding to Simpsons index, S_2), E_n (corresponding to rarified richness, S_n) and E_N (corresponding to observed species richness, S). To quantify the effect of passive sampling for the observed diversity gradients, we then calculated the difference between total diversity (E_N) and the diversity for a standardized number of individuals (E_n) for each sample. This difference represents the portion of the total diversity that is attributable to the fact that a sample exceeds the standardized number of individuals (Engel et al., 2022). We call it the "N-component" of diversity because it captures how differences in total abundance (N) translate to differences in sample diversity (due to passive sampling). Conversely, E_n can be considered the "SAD-component" because it reflects changes in the SAD and is unaffected by the total number of individuals in the sample (Engel et al., 2022).-Supplementary figure S1 shows how these components and metrics are linked to the individual based rarefaction curve.

Statistical analysis

We fitted Bayesian multilevel models (i.e. mixed effect models) to describe the elevational diversity gradients among the compiled datasets. Our models estimated the overall relationship between elevation and diversity (i.e. fixed effects) and variable model coefficients among gradients (i.e. random slopes and intercepts). In order to allow for commonly reported humped-shaped diversity patterns, we also included an additional quadratic term for elevation (also including random effects). Given the positive ranges of the response variables (E_2, E_n, E_N and N), we assumed log-normal error distributions and identity link functions for all models. We modelled the response variables E_N (i.e. the total diversity corresponding to species richness) and E_n (i.e. the SAD-component) using a multivariate version of the multilevel model, which means that besides the bivariate relationships with elevation we also estimated the correlations between the model coefficients of the two variables. This multivariate approach allowed us to predict the elevational pattern of the corresponding N-component (i.e. E_N- E_n) as a derived quantity from the multivariate posterior distribution. To do this, we calculated the difference between the posterior predictions of E_N and E_n for all posterior samples. For the other two response variables E_2 and N we fitted separate multilevel models. To assess whether any of the models supported mid-elevation humps, we evaluated the position of the predicted diversity maximum for all posterior samples. All models were fitted using the “brms” R package (version 2.18.0) for Bayesian inference (Bürkner, 2017, 2018), with 4 chains and 4000 iterations, using default priors. To achieve better model convergence, elevation was scaled and centered before entering the analyses. All analyses were done in R version 4.2.2 (R Core Team, 2022).

Results

Across all studies and for all three diversity metrics, we found predominantly decreasing diversity patterns with increasing elevation, although low-elevation humps or plateaus may also fall into the credible intervals of the global relationships (figure 2). The predicted diversity maxima of our quadratic models were mostly found in low elevations (Fig 4), which supports monotonic decreases as the overarching global pattern. Nonetheless, a number of individual gradients did clearly show mid-elevation humps, and a few datasets showed diversity increases with elevation (table 2). Overall, abundance was relatively unaffected by elevation at low and mid-elevations and only declined clearly at the highest elevations (figure 2). This global abundance pattern was accompanied by high variation at the gradient level, where about a quarter of the datasets described monotonic increases and a small fraction hump shapes (table 2). The weak abundance trend and the fact that the diversity gradient persisted, when we controlled for total abundance via the metrics E_2 and E_n, suggest that passive sampling effects are not the main driver of the elevational diversity pattern. Instead, the decline in sample diversity seems to be associated with changes in the size of the species pool and the shape of the SAD. Nonetheless, the steepness of the relationship increased from E_2 through E_n to E_N (Figure 2 B-D), which suggests that abundance does somewhat contribute to diversity pattern, by allowing more rare species to be sampled at low to mid elevations. This was also reflected by the elevational pattern of the N-component, which showed an overall declining pattern with a tendency for a plateau or shoulder in low to mid elevations (Figure 5).

Table 2. *Shapes of the relationships between abundance and elevation, and diversity and elevation at the gradient level, predicted from the multilevel models. Gradients with a predicted maximum at the beginning of the gradient were categorized as monotonic declining, those with a predicted maximum at the end of the gradient as monotonic increasing and those with a predicted maximum in-between as hump-shaped.*

Metric	**Gradient level patterns [number of gradients]**		
	Monotonic declining	**Hump-shaped**	**Monotonic increasing**
N	26	6	11
E_2	32	9	2
E_n	35	6	2
E_N	34	8	1

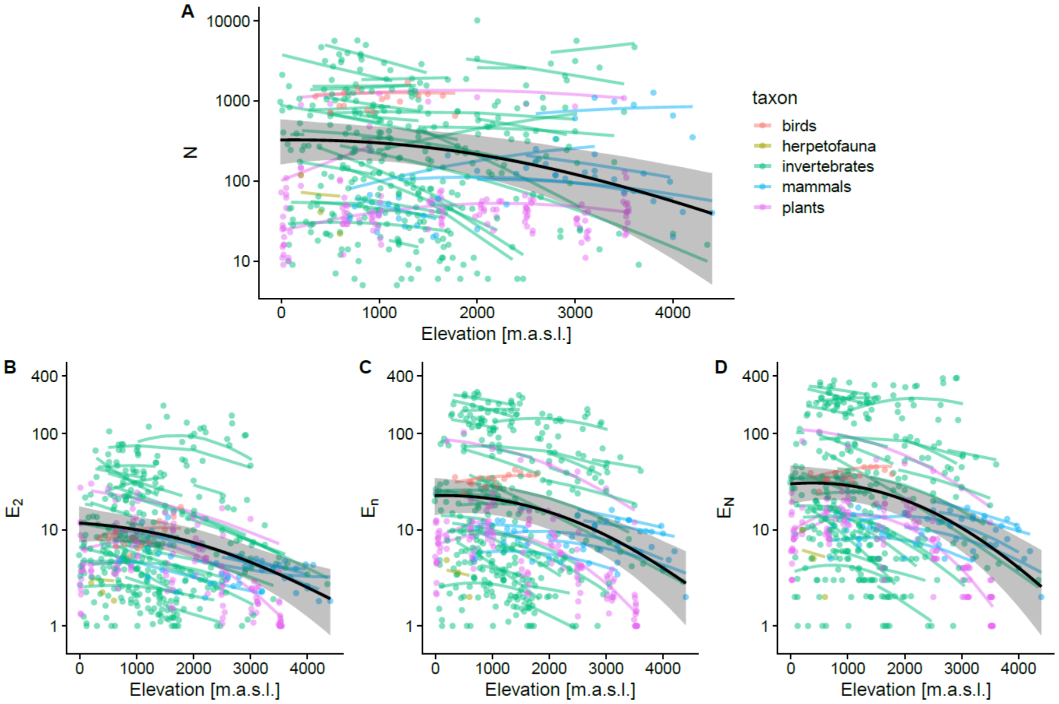

Figure 2: Elevational patterns of (A) total abundance, N, and (B-D) diversity. E_2 is the effective number of species (ENS) corresponding to Simpson's index (sometimes called S_{PIE}), E_n is the ENS corresponding to rarified richness and E_N is the ENS corresponding to species richness. The black line and grey ribbon show the mean and 95% credible interval of the posterior prediction of the global model fit. The coloured lines represent gradient-level predictions, and the points show the data. The colour indicates the taxonomic group. Elevation is shown in meters above sea level (m.a.s.l.).

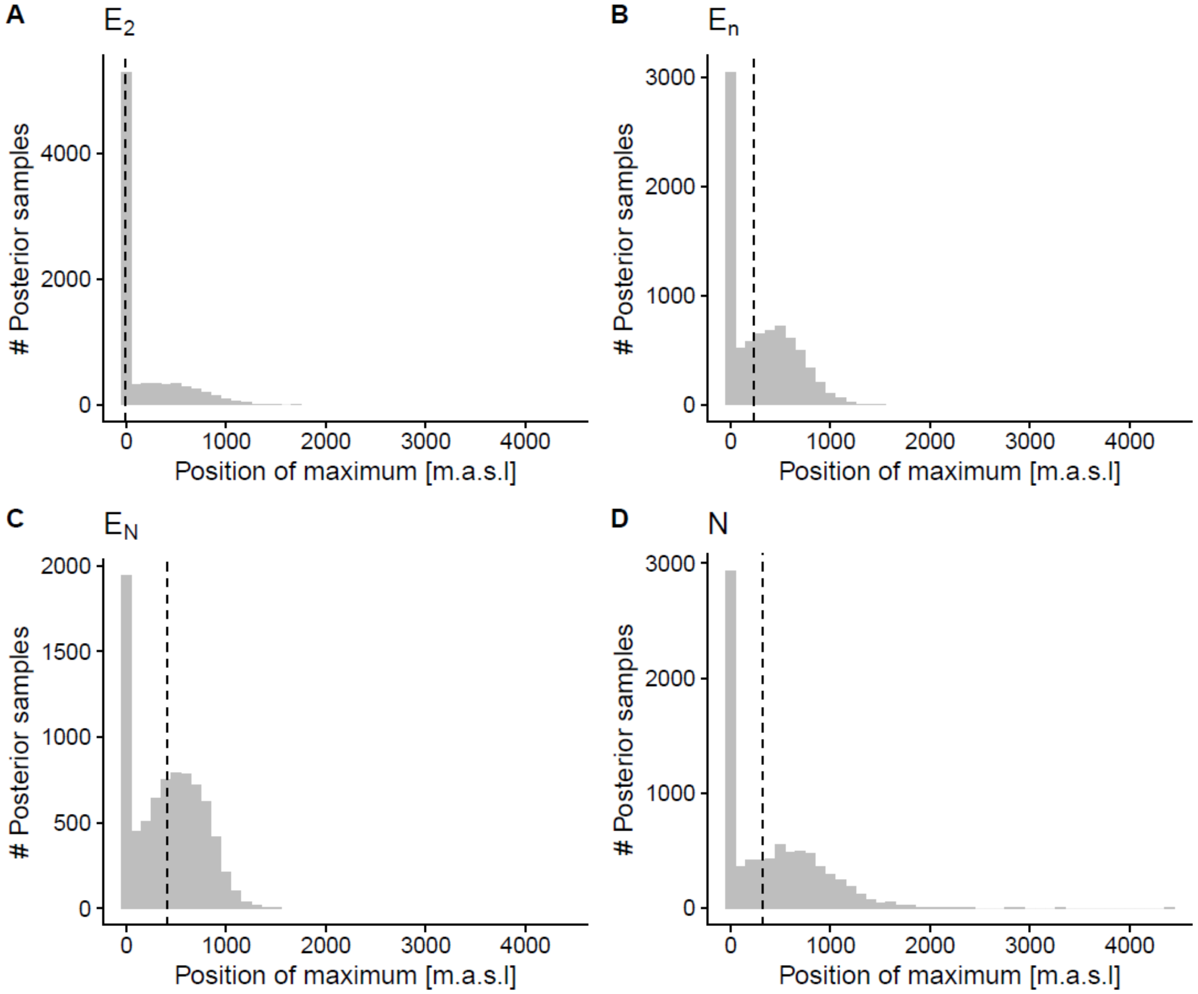

Figure 3: Histogram of the posterior samples for the position of the predicted global maximum along the diversity gradient for the metrics E_2 (A), E_n (B), E_N (C) and N (D). The binwidth is 100 m for all metrics. Dashed vertical line indicates the median value.

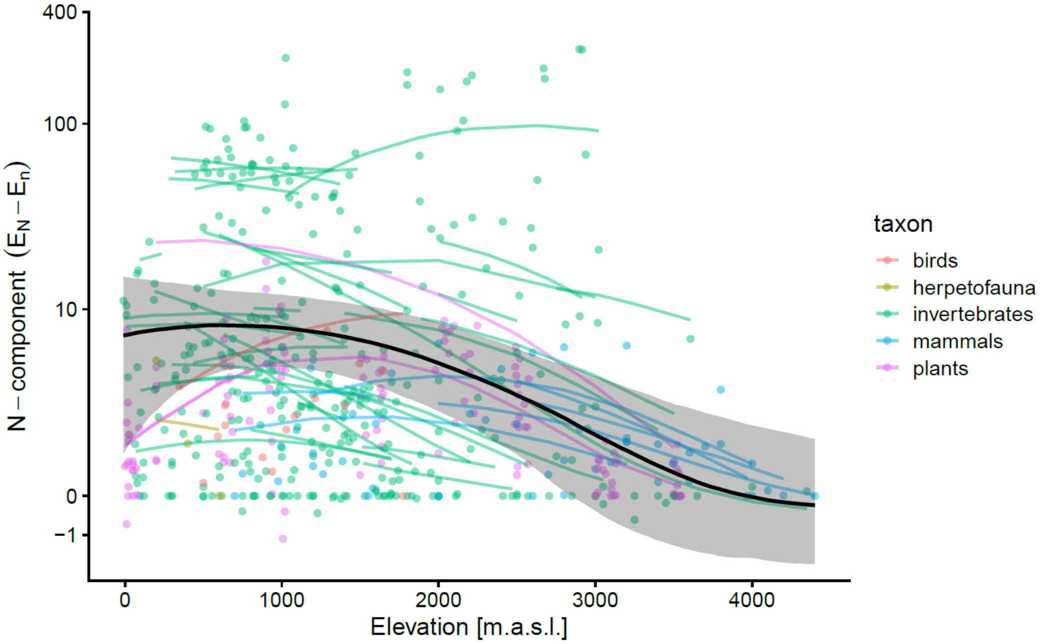

Figure 4: Elevational pattern of the N-component, which captures how differences in total abundance (N) translate to differences in sample diversity. It is calculated as the difference between the ENS transformation of total species richness (E_N) and the ENS transformation of rarefied richness (E_n).The black line and grey ribbon show the mean and 95% credible interval of the posterior derived from the multivariate multi-level model. The coloured lines represent gradient-level predictions, and the points show the data.

Discussion

The first systematic observations of declining species richness with increasing altitude date back to early naturalists like Darwin (1871) and Humboldt (1849). Since then many studies have reported very heterogeneous elevational patterns of species diversity but few papers have considered abundance patterns. In this global synthesis, we used abundance-based diversity measures to discern how the elevational diversity gradient is underpinned by patterns of total and relative species abundances. Confirming earlier findings, we found an overarching pattern of decreasing diversity patterns, with the possibility of low to mid elevation humps or plateaus. Importantly our results suggest that variation in total abundance is not a strong driver of this pattern, but rather the size and evenness of the regional species pool appear change along mountain slopes.

An important outcome from our study is that the passive sampling hypothesis can largely be rejected as a strong mechanism driving decreasing elevational diversity gradients. Under a scenario of passive sampling, abundance is expected to be more closely associated with a predictor such as elevation than species richness (Currie et al., 2004). Furthermore, the passive sampling hypothesis predicts that any diversity pattern should disappear in diversity metrics that control for the number of individuals (such as E_2 and E_n in our analysis). Our results do not show this. Nonetheless, we found that compared to the total diversity, the steepness of the gradient diminishes slightly for the standardized metrics, which is also reflected by the elevational pattern of the N-component of diversity (Figure 4). This suggest that at the sample scale, the abundance gradient enhances existing differences in species pool size. It is also noteworthy that on average abundance and total diversity peak at higher elevations than the standardized diversity metrics (Figure 3), which indicates that the relatively high abundances observed at low to mid elevations give rise humpier diversity patterns at the sample scale.

Although we modelled a global relationship across studies, we allowed for gradient-level variation in our analysis. While it has long been known that the elevational diversity gradient can take different shapes for different mountains and taxa, our findings are the first to show that elevational abundance trends are more varied than diversity trends (Table 1). One reason why there is little generality in the abundance relationship may be that elevation is not a driver per se, but instead correlates with a number of other environmental, anthropogenic and biogeographic drivers of biodiversity (McCain & Grytnes, 2010). Indeed, abiotic factors that likely shape abundance patterns such as precipitation, productivity, soil properties, and photosynthetically active radiation show extreme variation in montane areas and the direction, shape and strength of their relationships with altitude are highly variable among the mountains of the world (Körner, 2007). Here, we did not have enough studies to confidently discern how this heterogeneity can be explained by moderating variables such as taxon (a vast majority of datasets included in our analysis was on invertebrates). As more datasets may become available covering a wider taxonomic range, such analyses may become possible in future.

In conclusion, to our knowledge this study is the first quantitative synthesis on elevational diversity gradients to combine abundance-based diversity metrics using raw data from different original studies in a common multilevel model. Although we found some evidence that abundance trends contribute to elevational gradients at the sample scale - possibly making them humpier - our findings clearly reject abundance as an ultimate driver of the elevational diversity gradient. This finding from mountain systems is in line with a growing body of empirical syntheses that reject passive sampling as a strong driver for diversity patterns, e.g. as a mechanism underlying the island species-area relationship (Gooriah et al., 2021), species loss in fragmented habitats (Chase et al., 2020), productivity-diversity-relationships (Storch et al., 2018; Vagle & McCain, 2020) and biodiversity changes in space and time (Blowes et al., 2022). Future studies should focus on the eco-evolutionary processes that shape species pools along mountain slopes and elsewhere.

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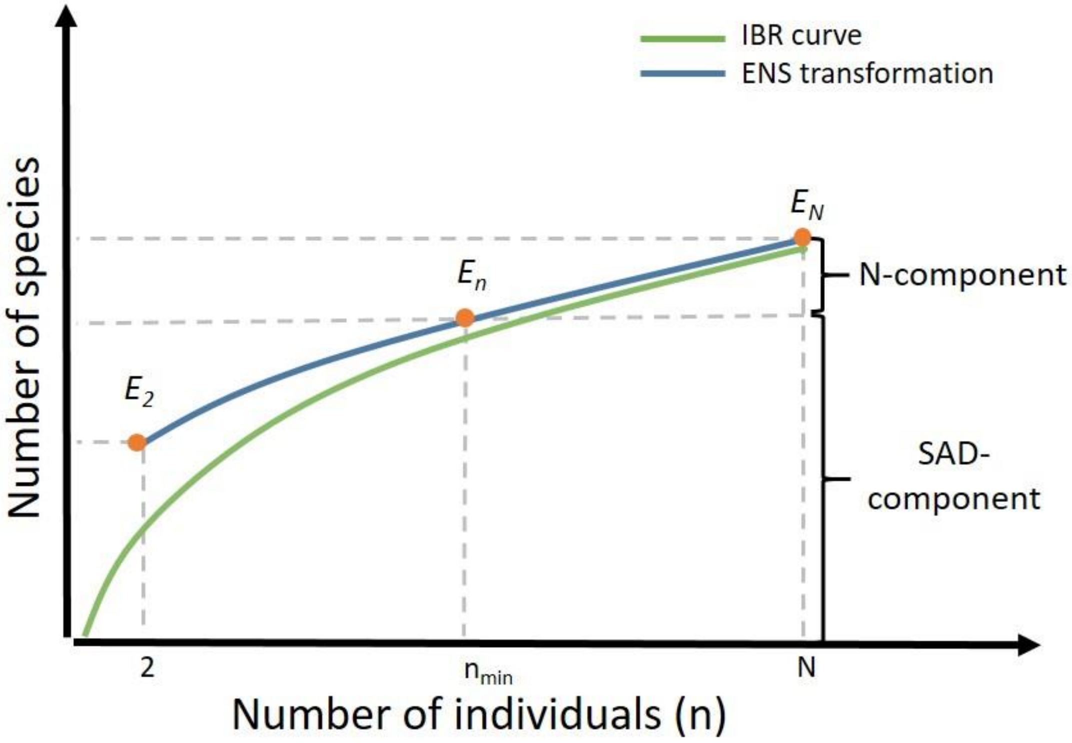
Supplementary Material Chapter 4



Supplementary figure S1: *Schematic drawing of an individual-based rarefaction (IBR) curve and the corresponding effective number of species (ENS) transformation, introduced by Dauby and Hardy (2012). The IBR curve is constrained by the values of n (i.e. it is bound to start at the origin). The ENS transformation is unconstrained on the vertical axis. Orange dots indicate the positions of the three diversity metrics described in the main text.* E_2 *is also known as* S_{PIE} *and corresponds to Simpson's index,* E_n *corresponds to rarefied richness for a standard number of* n_{min} *individuals and* E_N *corresponds to observed species richness). As they control for variation in total abundance,* E_n *values –like rarefied richness – reflect changes in the species abundance distribution (SAD) of the species pool. Therefore, we call them the "SAD-component" of diversity. The difference in diversity between* E_N *and* E_n *results from the fact that a sample usually exceeds the standard number of individuals* n_{min}*. This portion of the total diversity is attributable to passive sampling and we call it "N-component".*

Chapter 5 – Synthesis

Introduction

Species diversity is one of the most important quantities in ecological research and conservation, but its scale-dependent and multidimensional nature makes it hard to measure unambiguously (Chase et al., 2018). In this dissertation, I have developed new quantitative methods for the measurement of species diversity in the light of incomplete sampling and abundance variation, and I have applied them to datasets spanning latitudinal and elevational diversity gradients. Specifically, I have considered multidimensional and scale-dependent diversity patterns in terms of three broader components underlying diversity scaling relationships: 1) the numbers of individuals, 2) the species abundance distribution (SAD) of the regional species pool, 3) intraspecific spatial aggregation. As these components determine the shape of diversity scaling relationships, they are natural entry points into a better understanding of complex diversity patterns (He & Legendre, 2002). All approaches laid out in this dissertation were derived from the individual-based rarefaction (IBR) curve, which describes the non-linear scaling relationship between abundance and species richness (Hurlbert, 1971). Together with other work in this field (Chase et al., 2018; McGlinn et al., 2019), these approaches therefore form a methodologically coherent framework for the quantification of species diversity in time and space. The findings of this research contribute to addressing the ongoing biodiversity crisis by providing more accurate and comprehensive tools for quantifying species diversity and its change over space and time. In this synthesis chapter, I highlight some of the novel contributions of the dissertation, discuss limitations and shed light onto some of the avenues for future research.

New contributions of chapters 2 to 4

The second chapter of this dissertation addressed the longstanding debate on how to disentangle the contributors of beta-diversity variation along biogeographic gradients (Kraft et al., 2011; Tuomisto & Ruokolainen, 2012; Ulrich et al., 2017). Measures of sample differentiation such as beta-diversity are commonly used to assess the tendencies of species to be non-randomly distributed among samples (i.e. intraspecific spatial aggregation), however these measures are also strongly influenced by the size and evenness of the regional species pool, whereby diverse species pools typically exhibit high beta-diversity (i.e. spurious sample differentiation). This makes it difficult to interpret beta-diversity patterns where these latter components vary (e.g. along biogeographic gradients with differently sized species pools). I have argued that spurious sample differentiation is accompanied by low levels of sample completeness and that by accounting for differences in sample completeness, one can correct the species pool dependence of beta-diversity. Specifically, I developed a new beta-diversity metric (β_C) that utilizes coverage-based rarefaction to make beta-diversity comparisons at standardized levels of sample coverage (i.e. a measure of sample completeness). This contribution extends the method of coverage-based rarefaction from the scale of a single sample to the beta-scale and provides a much-needed sampling theory for beta-diversity. Using simulations of spatially explicit assemblages, I have shown that β_C remains unaffected by changes in the species pool, which allows for comparisons of intraspecific aggregation despite variation in the species pool size. Furthermore, I have used two empirical case studies, demonstrating that the magnitude of intraspecific aggregation does not change along a latitudinal gradient of forest plots. Unlike other null model approaches for beta-diversity, our method directly confronts the analyst with the estimated completeness of their samples, which may caution against unnecessarily strong conclusions when sample completeness is low. For example, in the case of the commonly used Gentry plots, this shows that the samples cover only a small fraction (10%) of the individuals in the underlying assemblages, and may therefore be of limited use for making inferences about their small-scale spatial structure (Tuomisto & Ruokolainen, 2012). In summary, this chapter has not only developed a new approach for the measurement of spatial aggregation, but it has extended our understanding of beta-diversity in the context of incomplete sampling.

The third chapter of this dissertation revolved around the question of how we can better quantify the absolute and relative contributions of abundance variation and changes in the regional species pool towards sample-level patterns in species diversity. Specifically, I developed an approach to dissect diversity changes using the effective number of species (ENS) conversion of the IBR curve. Complementary metrics derived from the IBR curve have long been used to disentangle these components (Chase et al., 2018; Hurlbert, 1971; McGlinn et al., 2019; Olszewski, 2004), however, it has been difficult to quantitatively combine the lines of evidence described by multiple metrics, as the corresponding effect sizes are not directly comparable. This is because metrics like rarefied richness, Simpson’s index and simple species richness differ in their numerical constraints. The novelty of my approach is that it uses the concept of effective numbers of species to decompose the diversity of a sample into a SAD-component and an N-component that are directly comparable. While effective numbers of species are commonly used in the context of other diversity measures (i.e. the Hill number framework, see Roswell et al., 2021), they are usually overlooked when it comes to rarefaction, although the methodological foundation (i.e. ENS rarefaction) was developed more than ten years ago (Dauby & Hardy, 2012). Using empirical case studies on two datasets spanning latitudinal diversity gradients in trees and marine reef fish, my paper highlights the utility of the new partitioning approach based on ENS rarefaction. Superficially, both taxa showed similar diversity gradients, however, my results revealed contrasting patterns underlying these gradients. While the diversity gradient in reef fish was mostly associated with variation in the number of individuals (86% N-effect), the diversity gradient in trees was to a larger extent associated with variation in the SAD (59% SAD-effect). These results suggest that local fish diversity may be limited by resource availability through the more-individuals effect, while in trees species pool effects are the larger determinant of local diversity. Not only does this paper add to the toolbox for biodiversity measurement and provide novel empirical insights into latitudinal diversity gradients, but it also deepens our conceptual understanding of the connections between Hill numbers, individual-based rarefaction and ENS rarefaction.

Finally, in the fourth chapter I applied some of the concepts developed in the previous chapter to an empirical synthesis of diversity and abundance patterns along elevational gradients. Specifically, I tested whether abundance trends along mountain slopes drive elevational diversity patterns through passive sampling effects. Although abundance-related mechanisms are often invoked as an explanation for elevational diversity gradients (McCain & Grytnes, 2010), I know of no other quantitative synthesis on this topic. My analysis combined community level abundance data that we compiled from the published literature in a common model. This kind of quantitative synthesis is novel in the context of elevational gradients, where it has been more common to use narrative reviews and syntheses on basic summary statistics (e.g. comparing the frequencies of hump shaped versus decreasing patterns). While my results reproduce commonly reported decreasing diversity patterns with increasing elevation (with considerable variation allowing for low to mid elevation peaks our plateaus), I was able to show that the overall diversity pattern largely persisted when abundance is controlled for. Furthermore, I showed that abundance patterns were more varied in strength and direction than diversity patterns. Together the results of this chapter suggest that passive sampling is not a major contributor to elevational gradients. Instead, changes the SAD and size of the regional species pool seem to drive the diversity patterns observed at the sample scale. Not only did this chapter employ novel approaches and produce new results on the generality of the elevational diversity gradient, but also it improves our understanding of the interrelated changes of diversity and abundance in general.

Discussion

The unifying objective of the previous chapters was to disentangle the components underlying species diversity patterns using a common set of tools derived from individual-based rarefaction. Although the specific questions and applications differed, the chapters revolved around a common set of ideas and tools to address the question of how species diversity responds to changes in the number of individuals, the size and SAD of the regional species pool, and patterns of intraspecific aggregation.

A common topic of all chapters been to quantify diversity in such a way that passive sampling effects can be disentangled from SAD effects. At first glance, it may appear that chapter 2 stands out because unlike the other chapters it is mostly concerned with non-random spatial distributions and questions of beta-diversity. However, at the core it uses the same principles of comparing IBR curves to infer SAD changes. Indeed, non-random spatial aggregation manifests as SAD differences between the alpha and the gamma scale (Olszewski, 2004). In other words, under clumped species distributions, the samples at the alpha are less diverse and less even than random draws from the gamma scale. Therefore, betaC actually measures SAD changes between scales, which come about due to non-random spatial distributions.

There is a lot of potential to further develop and combine the ideas that I proposed in the different chapters. For example, when I developed betaC I had not fully developed the effective number of species concept introduced in a subsequent chapter. Now, I am convinced, that it actually makes sense to apply the ENS transformation in the context of beta-diversity, as well. Although I have shown that betaC is a valid index for the degree of non-random spatial distributions, it would be useful if it were expressed in units of effective numbers of species. Then, one could ask questions like, what are the absolute and relative contributions of species pools and spatial aggregation toward Whittaker's beta diversity and its change. Furthermore, this would enable a comparison of all three components of diversity scaling at the same time, effectively dissecting total diversity into an N-component, an SAD-component and an aggregation-component. Incorporating the beta-scale in the ENS partitioning framework introduced in chapter 3 should be relatively straightforward but it exceeds the scope of this synthesis chapter. I might pick that up in the future. In a recent paper, we developed a similar approach that uses different species accumulation curves alongside the IBR-curve to partition out these three components. However, this approach requires a higher number of sampling scales and spatially mapped samples (McGlinn et al., 2021), which is rarely available and not very applicable for synthesis studies. Nonetheless, this method can provide a highly scale-explicit view into the diversity patterns of a given smaller system.

An important limitation of the species diversity concept used here and in community ecology in general is that it tends to ignore species identities. This means that diversity metrics draw inferences at the community level (e.g. richness and evenness) but they disregard occurrence and the population trends of any specific species. On the one hand, this makes it great for synthesis, because it allows to generalize patterns from very different systems (e.g. a comparison of trees and marine fish like in chapter 3). On the other hand, for any given system this level of abstraction may be too high to make meaningful recommendations for conservation and management. From a conservation perspective it is usually more important to conserve a particular species, a kind of assemblage or a given habitat type and configuration, rather than a particular SAD shape or degree of spatial aggregation. Therefore, the approaches that I presented here may be of limited use to some readers. Nonetheless, whenever diversity or species richness is believed to be of interest, aspects of scale-dependence including, relative and total species abundances, and spatial aggregation should be considered in order to draw appropriate conclusions (Chase et al., 2018).

Another limitation of IBR as a model for diversity scaling is that it assumes that individuals are drawn at random and independently of one another, much like blindly drawing differently coloured but otherwise identical balls from an urn (Gotelli & Colwell, 2001; Hurlbert, 1971). In reality however, species differ in their detection probabilities and they tend to occur in conspecific clusters. Furthermore, the concept of an individual is not always meaningful, for example in plants with vegetative propagation or ants that dwell in colonies (Gotelli et al., 2011). By combining IBR with sample-based accumulation curves (McGlinn et al., 2019, 2021) or drawing IBR curves at different spatial scales (like for betaC) one can assess the non-randomness of the samples. Concerning the differences in detection probabilities, there are new possibilities offered by the so-called integrated community occupancy models (Doser et al., 2022). This approach has the advantage that it can estimate occurrence patterns for multiple species and from heterogeneous data sources, whilst accounting for imperfect detection. I suspect that by modelling species dynamics instead of derived diversity metrics a lot of the ambiguity surrounding diversity can be avoided. Bridging between community level and species level perspectives on diversity change is something I would like to explore more in future work.

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Supplementary material for chapter 2

S1. Additional simulation

We carried out an additional simulation where we parameterized the species pool using the log-series distribution and variation in the alpha parameter. Additionally, we simulated different degrees of spatial aggregation by changing the mean displacement length (sigma) of the Thomas process (as opposed to the number of clusters as presented in the main text). We used all integers from 1 to 100 as alpha values for the log-series SAD which resulted into species pools of 5 to 344 species. We used the following sigma parameters to get increasingly aggregated species distributions: 1, 0.8, 0.4, 0.2, 0.1, 0.01. The number of clusters was set to 1 for each species. Like in the analysis presented in the main text, we found that Whittaker's beta and β_{S_n} responded to the change in SAD (alpha parameter), while β_C remained mostly unaffected by it (Fig S1).

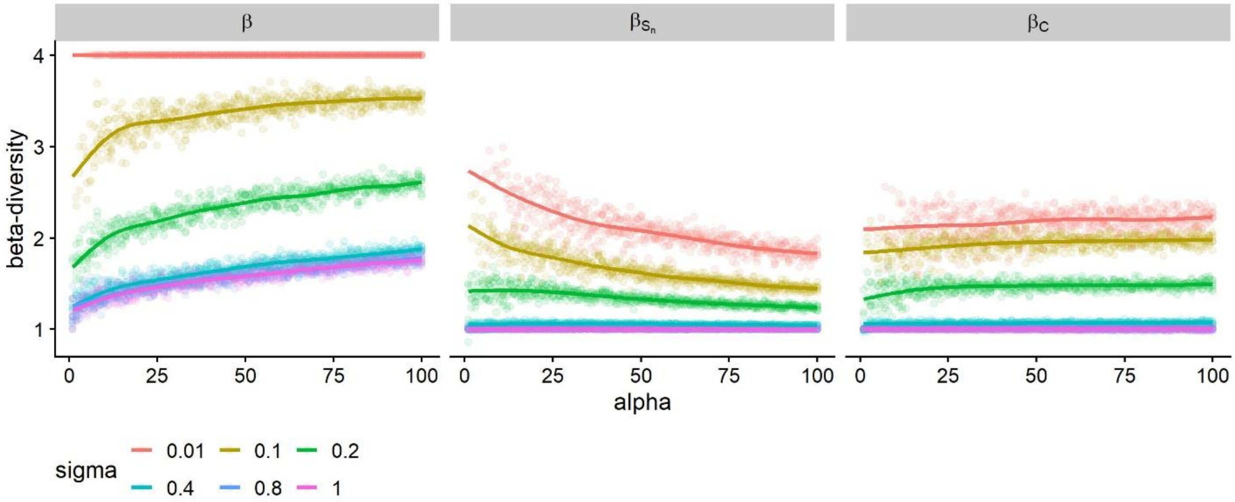


Fig S1: Response of Whittaker's β, β_{S_n} and β_C to changes in aggregation and species pool size from the additional simulation

S2. Beta-deviation

We also applied the Kraft null model to the simulated data. We used the code provided by Sebastian Tello provided on his website: http://jsebastiantello.weebly.com/r-code.html. We reshuffled the simulated site-by species abundance matrices 400 times, keeping the SAD and number of individuals per site constant. For each permutation, we calculated Whittaker's beta. Then we calculated beta-deviation as:

$$\beta_{dev} = \frac{\beta_{obs} - mean(\beta_{null})}{sd(\beta_{null})}$$

Where β_{obs} is the observed beta-diversity, $mean(\beta_{null})$ is the mean of the null distribution and $sd(\beta_{null})$ is the standard deviation.

Figure S2 shows how beta-deviation responds to our simulation parameters. Compared to β_C, it still shows some week species pool dependence for intermediate levels of intraspecific spatial aggregation.

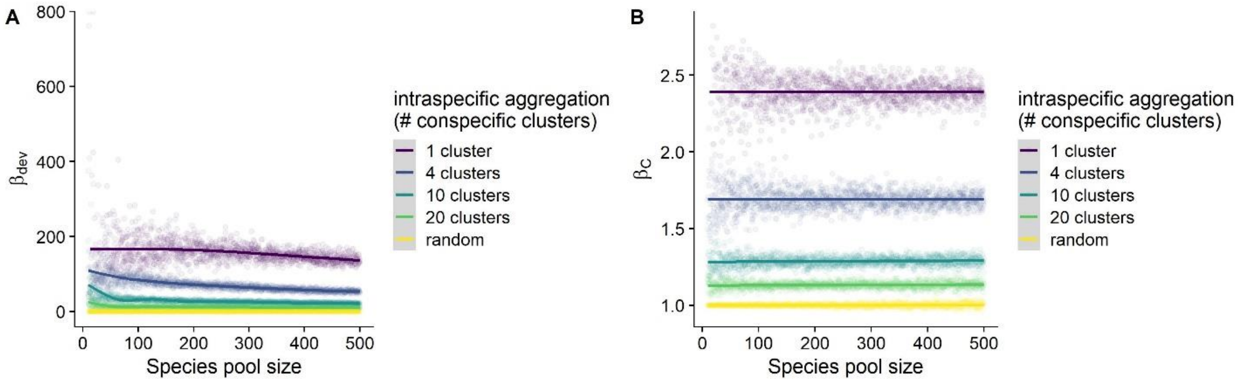


Fig S2: Response of (A) beta-deviation and (B) β_C to simulation parameters.

S3. Asymptotic behavior of β_C

Many authors have argued that metrics of beta-diversity should range between 0 and the number of sampling units (e.g., Jost 2007). β_C shows this behavior asymptotically. In the main text, we illustrate our method using an example with communities from differently sized species pools (Fig 2 and Fig 3). Although in both cases turnover is assumed to be at a maximum, the value of β_C does not reach the number of sampling units 2. This is because in this example the samples are not complete with respect to the total species pool (C_{target}= 0.8). β_C does range between 0 and the number of sampling units if target coverage is 100%. In this case β_C is exactly the same as Whittaker's beta, as both alpha and gamma scale curve have reached an asymptote that corresponds to the observed species richness.

Fig. S3 shows the same example but with an increased number of individuals sampled from each of the patches. Here, $\beta_C$can be calculated for a coverage of 1 (i.e. vertical dashed line) and its value becomes 2. When the value of is smaller for lower coverages, this merely reflects the fact that a fraction of the individuals in the assemblage are not covered by the species in the samples.

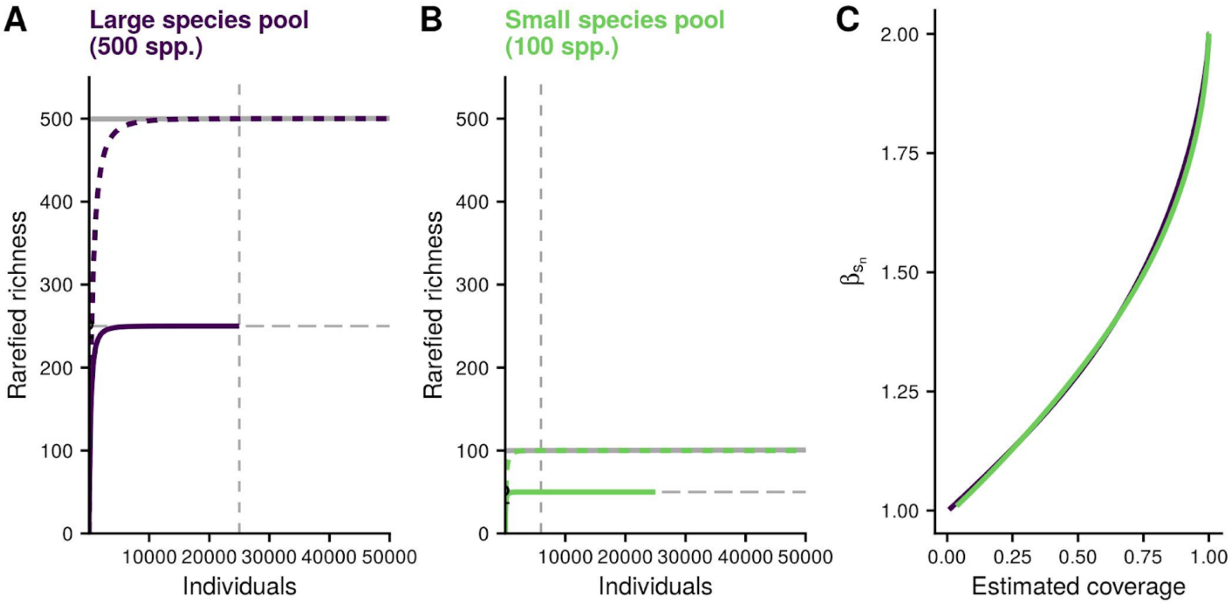
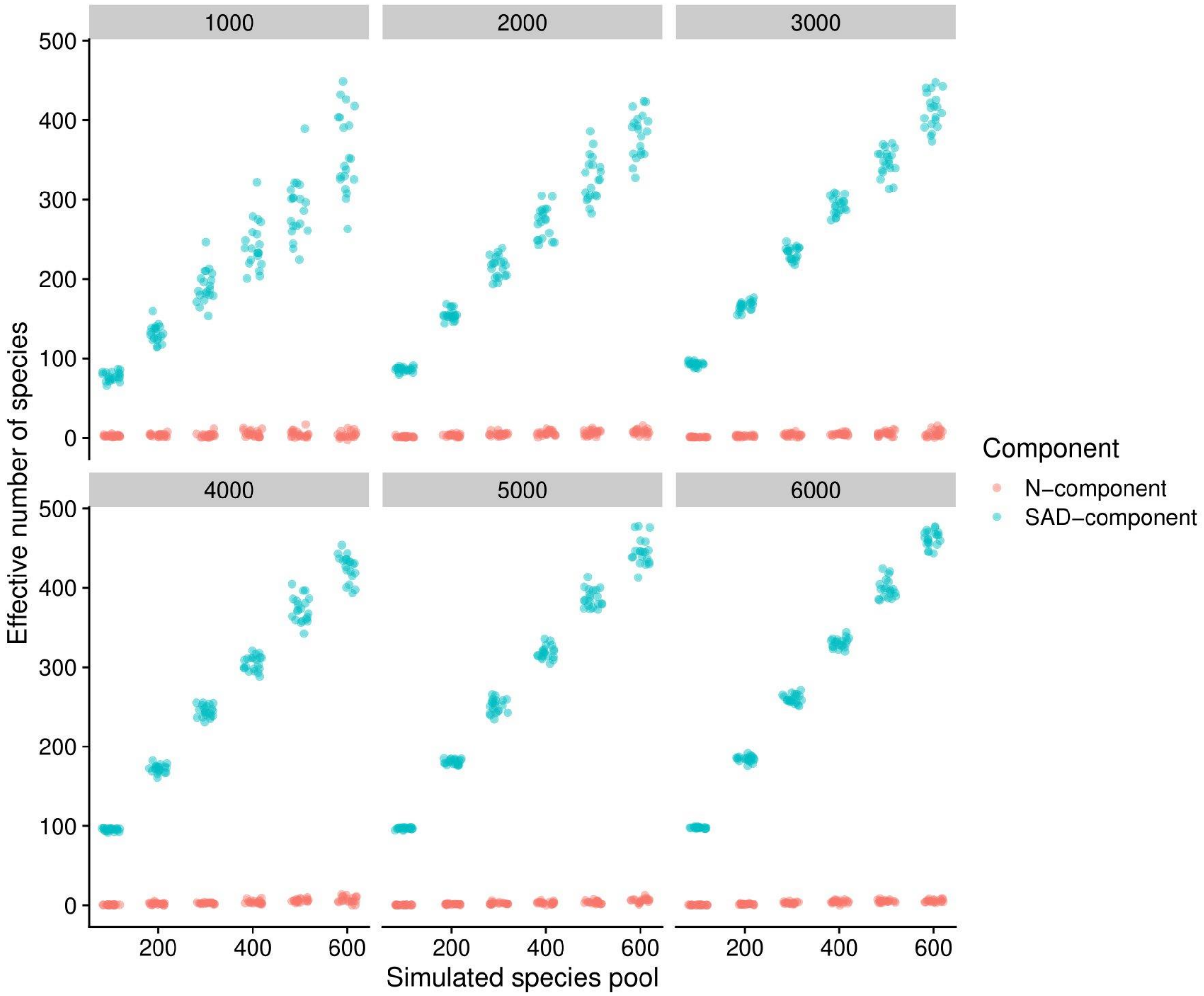
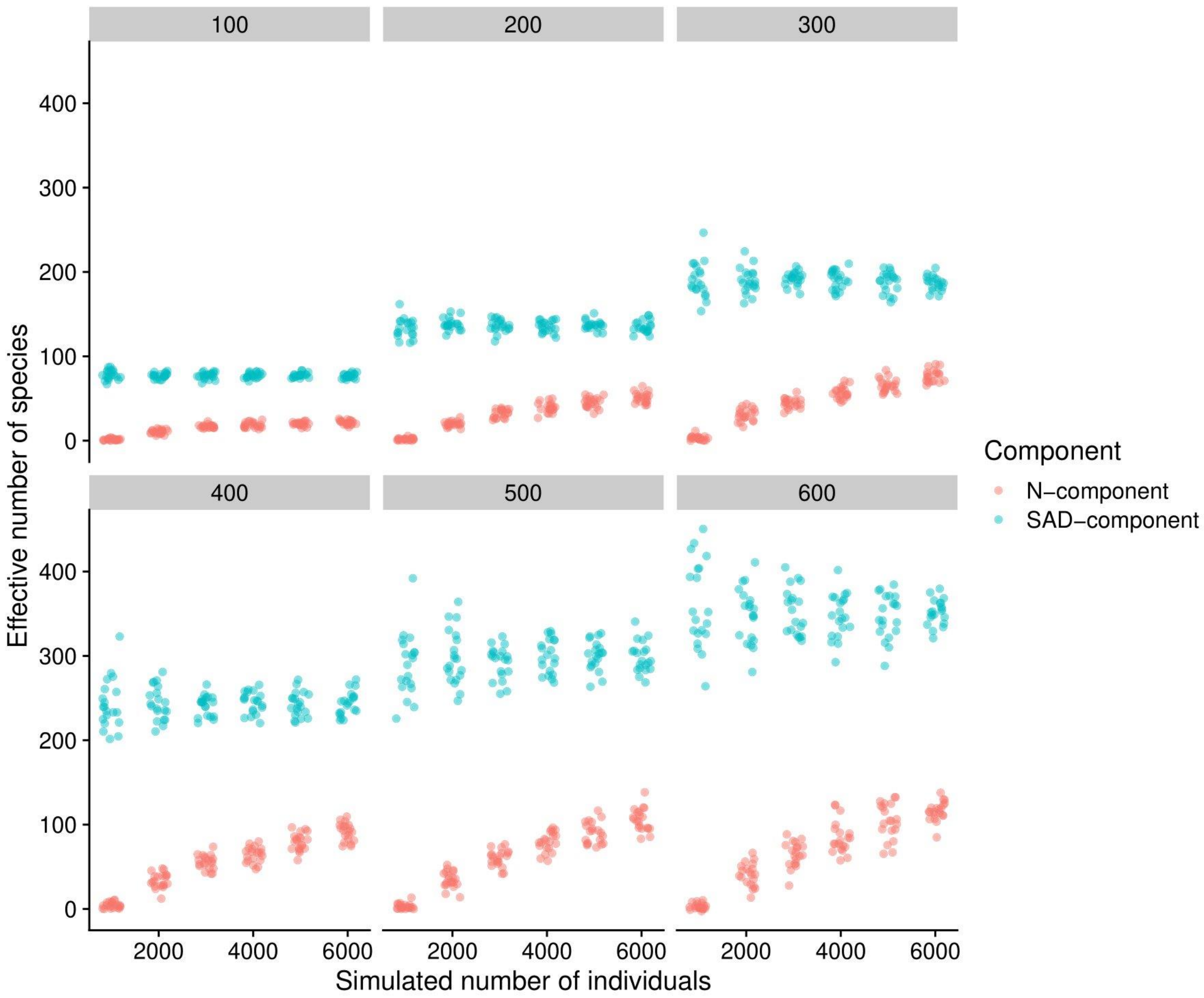


Fig S3: Under a scenario of complete turnover, β_C reaches the number of sampling units (here 2) when sample coverage is 100%

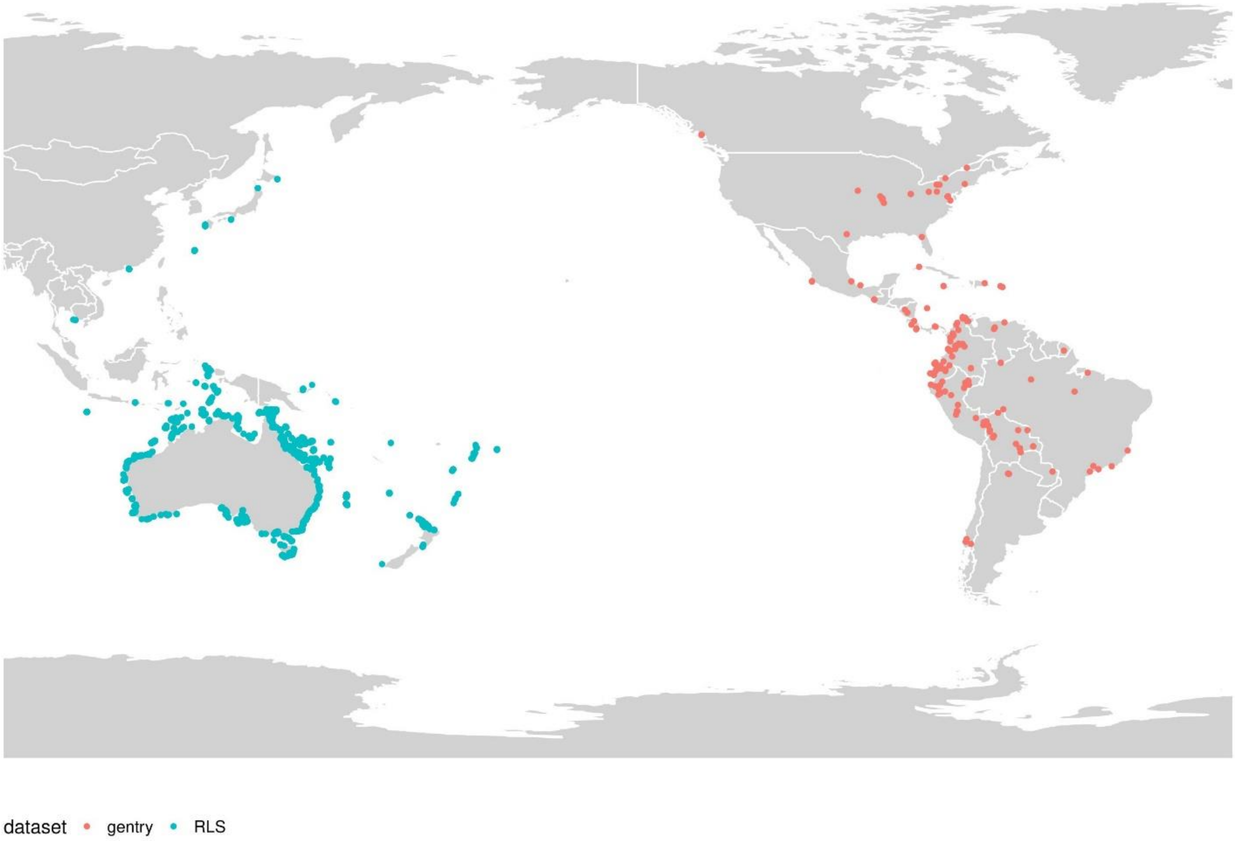
Supplementary material for chapter 3



Supplementary figure S1: Simulation of communities with different species pool sizes (horizontal axis) and total abundances (facets) and the corresponding response of the diversity components (vertical axis). The SAD-component (blue) responds to the species pool parameter, the N-component (red) remains unaffected by it.



Supplementary figure S2: Simulation of communities with different total abundances (horizontal axis) and species pool sizes (facets) and the corresponding response of the diversity components (vertical axis). The N-component (red) responds to the total abundance, the SAD-component (blue) remains unaffected by it.



Supplementary figure S3: Sampling locations include in the empirical case study. Red dots: Gentry forest plots (trees). Blue dots: RLS reel life survey (marine fish).

Author’s contribution

Chapter 2

Engel, T., Blowes, S. A., McGlinn, D. J., May, F., Gotelli, N. J., McGill, B. J., & Chase, J. M. (2021). Using coverage-based rarefaction to infer non-random species distributions. Ecosphere, 12(9), e03745. https://doi.org/10.1002/ecs2.3745

Conception/ Analysis: Engel, T (70%)
Writing: Engel, T (60%)

Chapter 3

Engel, T., Blowes, S. A., McGlinn, D. J., Gotelli, N. J., McGill, B. J., & Chase, J. M. (2022). How does variation in total and relative abundance contribute to gradients of species diversity? Ecology and Evolution, 12(8), e9196. https://doi.org/10.1002/ece3.9196

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Chapter 4

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Conference presentations and workshop participation

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Jan 2019	Poster presentation at the 9th Biennial Conference of the International Biogeography Society. Malaga, Spain
Dec 2018	Poster presentation at the iDiv Annual Conference 2018. Leipzig, Germany

Eigenständigkeitserklärung

Hiermit erkläre ich, dass ich die vorliegende Doktorarbeit mit dem Titel „Disentangling components of diversity scaling along biogeographic gradients“ eigenständig und ohne fremde Hilfe verfasst sowie keine anderen als die im Text angegebenen Quellen und Hilfsmittel verwendet habe. Textstellen, welche aus verwendeten Werken wörtlich oder inhaltlich übernommen wurden, wurden von mir als solche kenntlich gemacht. Ich erkläre weiterhin, dass ich mich bisher noch nie um einen Doktorgrad beworben habe. Die vorliegende Doktorarbeit wurde bis zu diesem Zeitpunkt weder bei der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt.

Thore Engel, Leipzig, 03.05.2023