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Methods, Tools, and Technologies

Disentangling nonrandom structure from random placement when estimating β-diversity through space or time

Daniel J. McGlinn[1] | **Shane A. Blowes**[2,3] | **Maria Dornelas**[4,5] | **Thore Engel**[2,6,7] | **Inês S. Martins**[4,8] | **Hideyasu Shimadzu**[9,10] | **Nicholas J. Gotelli**[11] | **Anne Magurran**[4] | **Brian J. McGill**[12] | **Jonathan M. Chase**[2,3]

[1]Department of Biology, College of Charleston, Charleston, South Carolina, USA

[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Leipzig, Germany

[3]Department of Computer Science, Martin Luther University Halle-Wittenberg, Halle (Saale), Germany

[4]Centre for Biological Diversity, School of Biology, University of St Andrews, St Andrews, Scotland

[5]MARE, Guia Marine Laboratory, University of Lisbon, Cascais, Portugal

[6]Institute of Biodiversity, Friedrich Schiller University Jena, Jena, Germany

[7]Department of Ecosystem Services, Helmholtz Centre for Environmental Research – UFZ, Leipzig, Germany

[8]Leverhulme Centre for Anthropocene Biodiversity, Berrick Saul Second Floor, University of York, York, UK

[9]Department of Mathematical Sciences, Loughborough University, Leicestershire, UK

[10]Department of Data Science, Kitasato University, Kanagawa, Japan

[11]Department of Biology, University of Vermont, Burlington, Vermont, USA

[12]School of Biology and Ecology and Mitchell Center for Sustainability Solutions, University of Maine, Orono, Maine, USA

Correspondence
Jonathan M. Chase
Email: jonathan.chase@idiv.de

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Abstract

There is considerable interest in understanding patterns of β-diversity that measure the amount of change in species composition through space or time. Most hypotheses for β-diversity evoke nonrandom processes that generate spatial and temporal within-species aggregation; however, β-diversity can also be driven by random sampling processes. Here, we describe a framework based on rarefaction curves that quantifies the nonrandom contribution of species compositional differences across samples to β-diversity. We isolate the effect of within-species spatial or temporal aggregation on beta-diversity using a coverage standardized metric of β-diversity (β_C). We demonstrate the utility of our framework using simulations and an empirical case study examining variation in avian species composition through space and time in engineered

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versus natural riparian areas. The primary strengths of our approach are that it provides an intuitive visual null model for expected patterns of biodiversity under random sampling that allows integrating analyses across α-, γ-, and β-scales. Importantly, the method can accommodate comparisons between communities with different species pool sizes, and it can be used to examine species turnover both within and between meta-communities.

KEYWORDS
aggregation, patchiness, rarefaction, sampling effects, scaling, species turnover, species-abundance distribution

INTRODUCTION

Ecologists are frequently interested in how the composition of species in a community changes across space or time (Daskalova et al., 2020; Magurran et al., 2019; Scheiner et al., 2011). The degree of change in species composition in assemblages across space or time is often referred to as β-diversity: localities or time periods with fewer species in common have higher β-diversity. Most conceptual explanations of β-diversity evoke processes that generate nonrandom spatial or temporal patterns of species aggregation (Leibold & Chase, 2018). Aggregation here refers to clustering whereby individuals occur near other individuals of the same species in time and/or space. For instance, two of the most discussed mechanisms underlying patterns of β-diversity are environmental filtering and dispersal limitation (Legendre et al., 2005; Leibold & Chase, 2018; Vellend, 2016). Both of these mechanisms increase aggregation of species distributions via conspecific clustering in space or time increasing β-diversity.

Although most attention has been focused on the nonrandom mechanisms underpinning β-diversity, β-diversity can also reflect random sampling effects of individuals and species taken from multiple points in space or time. Imagine we collect a sample of 40 individuals within a region or time period that supports up to 50 different species. Even in the improbable case that the numbers of individuals of each species are exactly the same (completely even), at least 10 species will be excluded from our sample because of the limited number of individuals. If we then compare that sample to another from a different location in space or time, a different set of 10 (or more) species will be excluded simply due to random sampling effects: the species composition of the two samples will differ entirely due to incomplete sampling. This phenomenon has been variously termed a "sampling effect" (e.g., Adler et al., 2005), a "rarefaction effect" (e.g., Palmer et al., 2008), and the "random placement model" (e.g., Coleman et al., 1982). The core idea is that the number of species observed in a sample is constrained by the number of individuals in that sample. Returning to our thought experiment, if the species have a more realistic abundance distribution, with many individuals of a few common species and many species with few individuals (i.e., rare species), these sampling effects on β diversity can be strong (Chase et al., 2018; Engel et al., 2021; Kraft et al., 2011; McGlinn et al., 2019). This example emphasizes that spatial or temporal β diversity is potentially underlain by two factors: (1) the nonrandom turnover of species, due to ecological mechanisms such as environmental filtering or dispersal limitation; and (2) the random turnover of species due to incomplete sampling, especially of rare species (i.e., sampling effects).

Most metrics of β-diversity conflate variation from both random sampling effects and spatially nonrandom mechanisms (Chao et al., 2023; Chase et al., 2018; Engel et al., 2021; McGlinn et al., 2019; Stegen et al., 2013). This means that the same observed change in β-diversity may be due to different underlying mechanisms, sometimes referred to as a "many-to-one problem," which are common in ecological studies (Frank, 2014; Scholes, 2017). Specifically, random turnover can occur where there are changes/differences in other nonspatial components of diversity, such as the species abundance distribution and size of the regional species pool and the total number of individuals. To illustrate this, consider the three hypothetical scenarios in Figure 1 using Whittaker's (1960) β-diversity ($\beta_S = \gamma/\overline{\alpha}$, where γ is the regional, and $\overline{\alpha}$ is the average of local diversity). In each scenario (Figure 1a–c), a shift in a different component of community structure results in a doubling of Whitaker's β-diversity (from 1 to 2). In the first two cases (Figure 1a,b), β-diversity increases due simply to random placement of individuals resulting either from a shift in the species-abundance distribution (SAD), for example, a decrease in evenness or, from a decrease in the total number of individuals (N). In the third case, the same magnitude of shift in β_S is due to an increase in conspecific aggregation (Figure 1c). This "many-to-one" effect is particularly problematic when trying to link changes in β-diversity to hypotheses that evoke changes to conspecific clustering due to environmental filtering or dispersal limitation. To link these

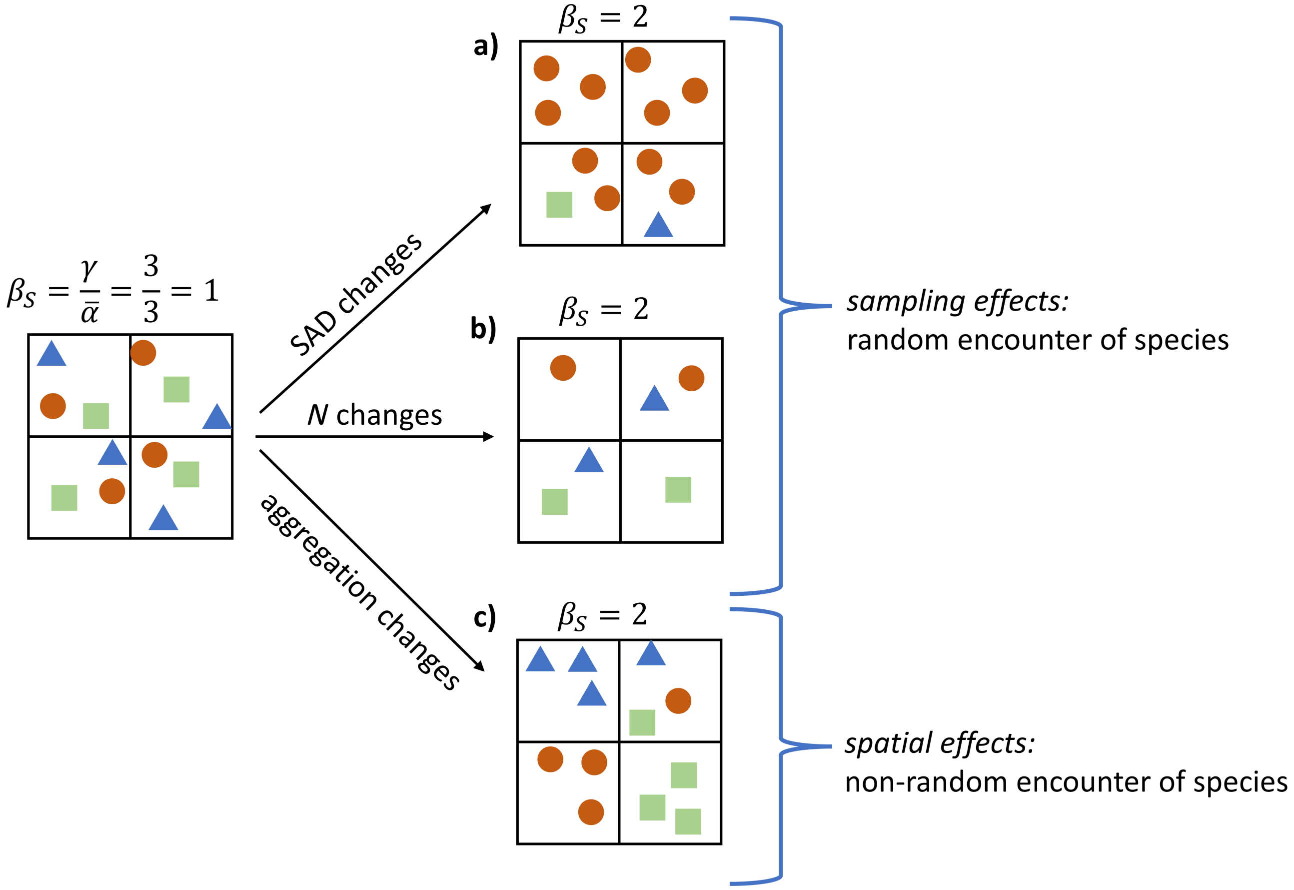

FIGURE 1 Cartoon communities that illustrate how random sampling effects and nonrandom spatial effects can result in identical values of Whittaker's β-diversity (β_S), where $\bar{\alpha}$ is average sample richness across plots (small boxes) and γ is total species richness in a site (large boxes). The different symbols represent individuals of different species. Panels (a) and (b) illustrate changes in community structure that are consistent with a random sampling model in which spatial β increases either (a) because the regional species-abundance distribution (SAD) is less even or (b) because there are many fewer individuals. Panel (c) illustrates how a spatially nonrandom process such as environmental filtering results in conspecific aggregation producing an identical value of β_S.

mechanisms to β-diversity, it would make sense to focus on patterns of β-diversity that reflect only changes in conspecific aggregation after controlling for changes in *N* or the SAD (which we refer to as sampling effects). One consequence of β-diversity metrics confounding both random and nonrandom variation is that most β-diversity metrics can increase as aggregation decreases if *N* is decreasing or the SAD is becoming less even, for example. It is important to note that as Figure 1 demonstrates, the SAD, *N*, and aggregation effects cannot be disentangled completely (this is particularly true when the number of individuals and/or the number of samples is small). For example, the random removal of individuals inevitably also leads to a change in the spatial point pattern and SAD seen at the sample scale (Figure 1b). Therefore, we propose a metric that isolates aggregation effects after controlling for SAD and *N* effects. Priority is given to SAD and *N* effects because they provide a more parsimonious null explanation (sampling effects) for why species composition has changed.

It is important to emphasize that sampling effects potentially influence all β-diversity metrics. Any metric of β-diversity that does not explicitly consider the process of sampling is sensitive to sampling effects. So regardless of whether turnover is calculated using presence–absence versus abundance data, is examined in space or time, or using pairwise versus multisite metrics, if the goal of the analysis is to link patterns of compositional change to mechanisms that generate nonrandom conspecific occurrence patterns, then sampling effects should be controlled for in the measurement of β-diversity. Other authors have recognized this and proposed a randomization algorithm to try to control for sampling effects on β-diversity (Chase et al., 2011; Kraft et al., 2011; Myers et al., 2013, 2015). Yet, continued debate as to exactly how to develop those randomizations, and just what the deviations mean (Kraft et al., 2012; Qian et al., 2012, 2013; Tucker et al., 2016; Xu et al., 2015), indicates that a more general solution is necessary.

In this paper, we describe a framework for quantifying the nonrandom contribution of species compositional differences across samples to β-diversity. This framework can be applied to any question related to measuring compositional variation (i.e., β-diversity) across samples, whether it be within a given (relatively homogenous) meta-community, across an environmental gradient, or through time. The approach allows us to differentiate the contribution of nonrandom species compositional shifts from the effects of sampling properties due to random placement to changes in β-diversity. As a result, we can quantify and compare compositional shifts among samples through space or time, and potentially relate these to other features of the system (e.g., changing spatial or environmental conditions). Here, our primary purpose is not to review and/or unify all metrics and measures of β-diversity, nor to advocate for a single superior metric, both of which have been attempted (Chao et al., 2012, 2023; Tuomisto, 2010). Rather, we promote a framework for measuring the relative influence of sampling and nonrandom associations that underlie β-diversity among samples, regardless of whether it is measured within or across landscapes, through time, or any combination thereof. Furthermore, rather than using different concepts and tools, we show how a single conceptual framework can identify the key components underlying variation in species composition.

First, we describe a simple framework that uses rarefaction curves to decompose β-diversity into components due to sampling effects, and those that are due to nonrandom aggregations of species. Second, we show that the framework can be applied to multiple, related questions about how species composition varies across samples.

A UNIFIED FRAMEWORK FOR DISSECTING THE NONRANDOM CONTRIBUTION OF SPECIES COMPOSITIONAL VARIATION TO β-DIVERSITY IN SPACE AND TIME

The components of our framework are not new. The framework is based on a long history of rarefaction and accumulation curves that depict how species numbers increase with increasing sampling effort (Preston, 1960; Sanders, 1968). For example, Kobayashi (1982, 1983) showed how spatial aggregation could be quantified from rarefaction curves by comparing subsets of spatially explicit samples to the entire range of spatially randomized samples. Likewise, Gotelli and Colwell (2001) showed how comparing accumulation or "collectors" curves that retain spatial information about the distributions of individuals to individual-based rarefaction curves could provide an indicator of the degree to which aggregation influenced spatial patterns of species accumulations (see also Cayuela et al., 2015; Chase et al., 2018; Chiarucci et al., 2009; Crist & Veech, 2006; He & Legendre, 2002; McGlinn et al., 2019). Plotkin and Muller-Landau (2002) demonstrated analytically that species turnover is strongly linked to variation in the SAD and conspecific aggregation. Finally, Olszewski (2004) explicitly discussed how the comparisons between spatially explicit and randomized rarefaction curves could be used as an index of β-diversity (see also Crist & Veech, 2006; Dauby & Hardy, 2012). These perspectives have been more recently formalized using individual-based rarefaction curves (and related diversity curves) to disentangle nonrandom structure from random placement underlying β-diversity within a given set of environmental conditions (i.e., a meta-community) (Chase et al., 2018; Engel et al., 2021; McGlinn et al., 2019, 2021). Specifically, Engel et al. (2021) developed an approach that uses coverage-based rarefaction to compare meta-communities at similar levels of sample completeness. Here, we generalize this approach and apply it to questions examining β-diversity among different kinds of samples, such as sites across a strong environmental gradient, or when quantifying temporal β-diversity.

Our framework is designed for one of the most common data types available to community ecologists—a sample-by-species matrix. Each sample contains a vector of abundances of all species sampled from a given assemblage and comes from a given local site. Samples can be collected across multiple sites (a site-by-species matrix) or across multiple time periods (a time-by-species matrix), or a combination of the two. For simplicity, we illustrate the different steps of the approach with samples taken from two spatial locations or time points in Figure 2, but it can be generalized to any number of samples. We assume that the communities being compared are sampled in such a way that they have the same sample effort, that is, the spatial and temporal grain, extent, and sample arrangement are equal across communities (or can be standardized to such). Here, we define a single sample as the α-scale, and the sum of samples as the γ-scale; however, other accumulation schemes are also possible, so long as the α-scale is a subset of the γ-scale.

Step 1: Create a rarefaction curve for the sum of all samples: γ-scale

If we pool the two (or more) samples, we can calculate the γ-scale rarefaction curve (solid, thick black line in Figure 2). This curve shows the number of species for a random sample of individuals from the whole meta-community,

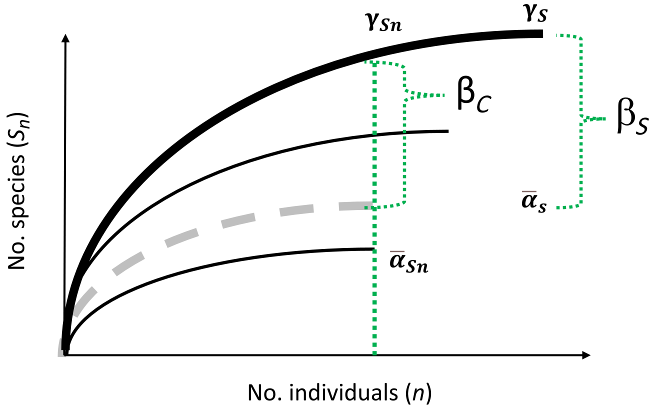

FIGURE 2 Individual-based rarefaction curves at the α- and γ-scales. Solid thin black lines depict two α-scale curves, with their average shown by the dashed thick gray line; the thick solid black line shows the γ-scale curve, which is calculated by pooling the two α-scale samples. Whittaker's β_S is calculated as the ratio of γ_S (total species richness) and $\bar{\alpha}_S$ (average sample richness). In contrast, coverage-based β_C controls for the number of individuals sampled (n) by using the ratio of γ_{S_n} and $\bar{\alpha}_{S_n}$. When comparing meta-communities, n should be chosen such that it provides a target degree of coverage that adjusts for variation in the regional (species pool) species-abundance distribution (eq. 5 from Engel et al., 2021).

or time series; for any sample of n individuals, S_n is the expected number of species in that sample. This type of rarefaction curve is sometimes referred to as an individual-based rarefaction curve or random sampling model. The curve and its variance has been derived analytically for sampling without replacement (Heck et al., 1975; Hurlbert, 1971; see Coleman et al., 1982 for formulation for sampling with replacement). Here, because we calculate rarefaction using all samples, the γ-scale curve represents a "null expectation" of the number of species for n individuals, when all individuals of all species occur randomly across the samples (in space or time).

Step 2: Create a rarefaction curve for each individual sample and average them: α-scale

Next, we calculate the rarefaction curves for the individual samples (Figure 2, solid thin black lines) and average them to obtain the α-scale rarefaction curve up to the number of individuals (n) that provides the target level of coverage (dashed thick gray line; Engel et al., 2021). Here, coverage refers to how close the γ curve has come to a hypothetical asymptote (i.e., it is an estimate of sample completeness; Chao & Jost, 2012).

Step 3: Compare the α and γ-scale curves to estimate the β-scale patterns

The classical Whittaker's β_S metric is calculated as $\gamma/\bar{\alpha}$, where $\bar{\alpha}$ is the average sample richness (Whittaker, 1960). Within our framework, these values are represented by the ends of the rarefaction curves (i.e., the average number of species per site [$\bar{\alpha}$], and all species observed across all sites in a region or time points [γ], Figure 2).

To estimate nonrandom spatial structure, we compute the ratio of γ_{S_n} and $\bar{\alpha}_{S_n}$ (dashed line), which we call coverage-based β diversity (β_C; Engel et al., 2021). This metric standardizes for sampling effects because we use the same value of n for the average α- and γ-scale rarefaction curves. As noted above, the value of n is chosen to meet a particular level of coverage it provides at the γ-scale.

To illustrate the behavior of these metrics, we simulated four scenarios similar to those shown on Figure 1, and calculated β_S and β_C (Figure 3). All scenarios have 50 species in the regional pool, but they vary from the starting community in either their evenness, total number of individuals, or conspecific aggregation. When individuals of all species are distributed randomly and only the evenness of the SAD decreases or the total number of individuals decreases, we see that the average α-scale curve (dashed gray line) falls directly on top of the γ-scale curve (solid black line, Figure 3e–g), and low evenness and fewer individuals are associated with increases in β_S, but β_C is equal to 1 in both cases. However, when we add nonrandom structure via species aggregation, the α- and γ-scale IBR curves diverge, and both metrics are greater than 1.

If species are randomly distributed among sites, then species will likely be sampled at all sites, and the α- and γ-scale curves will fall on top of each other. However, if species display conspecific aggregation (i.e., individuals within a species are clumped) such that they are nonrandomly distributed in space or time, then the α-scale curve will fall below the γ-scale curve (as in Figure 3h), because new species will be encountered across different sites or time points due to the within-species aggregation, pulling the α-scale curve down relative to the γ-scale curve. The resulting ratio of γ_{S_n} and $\bar{\alpha}_{S_n}$ becomes larger than unity ($\beta_C > 1$) due to intraspecific aggregation among sites or time periods. Thus, β_C reflects the degree of nonrandomness in the spatial or temporal distribution of species within the domain of $(0, \infty)$.

The example in Figure 3d shows a case where there is a nonrandom distribution of species composition among samples due to conspecific aggregation, and $\beta_C > 1$. However, it is also plausible that the α- and γ-scale curves could completely overlap, in which case we

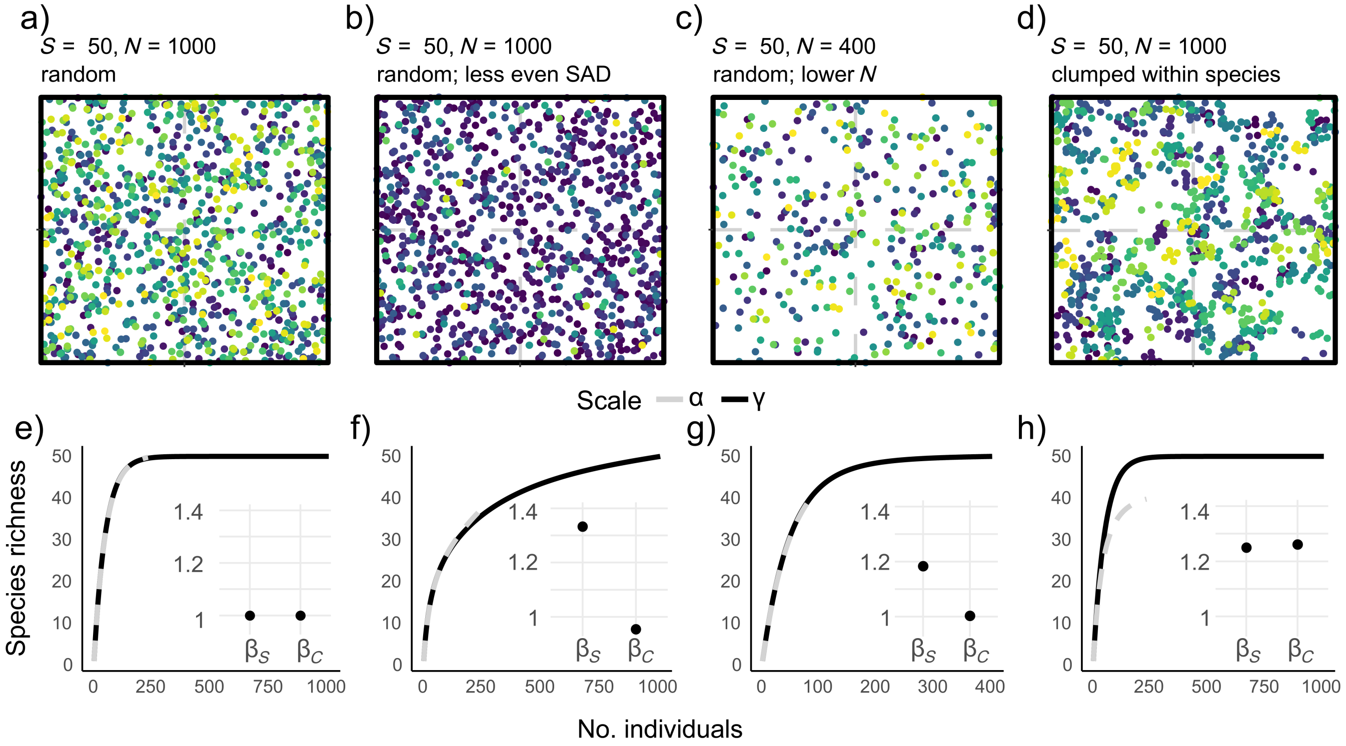

FIGURE 3 Quantitative illustration that β_S responds to changes in evenness and the total number of individuals, whereas β_C only responds to changes in within-species aggregation. Simulated communities are shown in panels (a–d) in which different colored dots represent individuals of different species. The landscape (γ scale) is divided into four quadrats (α scale, dashed gray lines). Panels (e–h) show the corresponding rarefaction curves associated with each artificial community for the γ- (solid black line) and average α-scales (dashed gray line). Inset on these panels is the value of each β diversity metric described. Note that $\beta = 1$ means species composition does not vary among samples.

would conclude that even though there is β-diversity (i.e., $\beta_S > 1$), this is simply due to random placement effects ($\beta_C = 1$). Finally, species can also show conspecific segregation (i.e., individuals within a species are overdispersed more than random), where the α-scale curve falls above the γ-scale curve, and $\beta_C < 1$ (not shown).

One additional benefit of β_C (that is not illustrated in Figure 3 but described in detail in Engel et al., 2021) is that this metric is unbiased when comparing β-diversity across meta-communities that differ in the size of their species pools (e.g., in temperate vs. tropical environments, or across strong environmental gradients). This is accomplished by computing β_C within each meta-community at the same level of sample coverage or completeness (Chao & Jost, 2012). In effect, ensuring that γ-scale sample coverage is the same for all meta-communities means that the value of n (the number of individuals for which γ_{S_n} and $\overline{\alpha}_{S_n}$ are calculated) varies among meta-communities.

To summarize, traditional measures of variation in species composition across area or time (β_S) are shaped by both random and nonrandom sampling processes, and we can isolate the nonrandom structure in space or time in determining that scaling by calculating β_C (Table 1). Furthermore, we can evaluate these β-diversity measures for a wide variety of questions concerning species compositional shifts in space and time. We provide R code to calculate classical β_S and β_C (as well as several other β metrics which we do not show here for simplicity) in mobr::calc_beta_div (McGlinn et al., 2024). The target level of coverage can be specified using the "C_target_gamma" argument.

ONE APPROACH, MANY QUESTIONS: SOME EXAMPLE APPLICATIONS

There are several benefits to our approach. Rarefaction curves provide an intuitive visualization of α- and γ-diversity patterns, the shape of the SAD, and the degree of variation in species composition that exists between samples. Moreover, the same family of measures can be used to estimate β-diversity, and to differentiate between random placement and nonrandom structure leading to biodiversity scaling for multiple related questions.

TABLE 1 Multiplicative β diversity metrics and the effects that they capture.

Metric	No. individuals sampled (n)	Effect controlled for	Effects captured
β_S (Whittaker's)	Regional n versus average local n	None	SAD, N, and aggregation
β_C (coverage)	Regional n equals local n and corresponds to a target level of coverage. Across meta-communities, coverage is fixed but n may vary.	N and SAD (evenness and size of pool)	Aggregation

Note: Species abundance distribution (SAD) effects are due to changes in species evenness and/or the size of the species pool, N effects refer to changes in richness due to variation in the number of individuals sampled, while aggregation effects refer to changes in richness due to variation in how individuals are spatially or temporally distributed (clumped, random, or overdispersed).

We illustrate some of this potential using a case study. We examined compositional variation in bird diversity between natural and engineered riparian habitats using a subset of data from the Central Arizona-Phoenix Long-Term Ecological Research site (Warren et al., 2022). We focus on riparian habitats where water permanence was perennial, and contrast sites in engineered settings (including a landscaped riparian preserve, a constructed wetland, and a water retention area along the Salt River, each surrounded by urban or agricultural areas) with those in more natural environments (located along perennial river reaches and surrounded by desert). Point count surveys with a 40-m fixed radius were conducted by trained observers that recorded all birds seen and heard; we analyzed samples collected in spring between 2001 and 2016. Before calculating our metrics, we ensured that sample effort was consistent across all sites and years; this meant three sites were retained from each habitat (engineered and natural), and data from 2003 and 2009 were discarded due to missing samples.

Using these effort-standardized data, we address four questions examining how random and nonrandom components contribute to patterns of β-diversity through space and time: (1) Does the total spatiotemporal variation in community composition differ between engineered and natural habitats? (2) How does spatial variation in community composition change through time in each of the two habitats? (3) Does the temporal variation in community composition differ between engineered and natural habitats? (4) Are there compositional differences between (rather than within) engineered and natural habitats, and do any differences change through time?

(Q1) Does the total spatiotemporal variation in community composition differ between engineered and natural habitats?

We used all site-year combinations within each habitat to examine total spatiotemporal variation in community composition. γ-Scale rarefaction curves combine all the samples across space and time within habitats, and show that the engineered habitat had more individuals, but fewer species than the natural habitat (Figure 4a). To examine spatiotemporal variation, we defined the α-scale as a single site-year combination within a habitat (Figure 4a inset shows α- and γ-scale curves). The greater number of species in the natural habitat compared with the engineered habitat resulted in higher β_S in natural habitats. However, this pattern was reversed for β_C when the influence of sampling effects was removed from the calculations (Figure 4b), meaning that aggregation in time and space was similar in the engineered and natural habitats.

(Q2) How does spatial variation in community composition change through time in each of the two habitats?

Figure 5 shows the pattern of spatial β-diversity in engineered and natural habitats through time. β_S increased through time for the natural sites, indicating that those communities were becoming more different from one another through time (opposite to the oft expected pattern of biotic homogenization, where communities become more similar through time and spatial β diversity declines). There was no similar trend in spatial β_S of the engineered sites, and by the end of the time series (but not the beginning) the engineered sites had lower levels of β_S than the natural sites. However, this pattern qualitatively changed when the influence of nonrandom patterns was explicitly considered. β_C indicates that species became less aggregated within engineered sites through time, suggesting biotic homogenization after random-placement mechanisms were controlled, and no change in β_C in the natural habitat. Combined, these results suggest the apparent pattern of increasing differentiation in the natural habitat was mostly driven by sampling effects (e.g., altered numbers of individuals, and/or rare species), and that there was a weak decrease of within-species aggregation across sites in the engineered habitat.

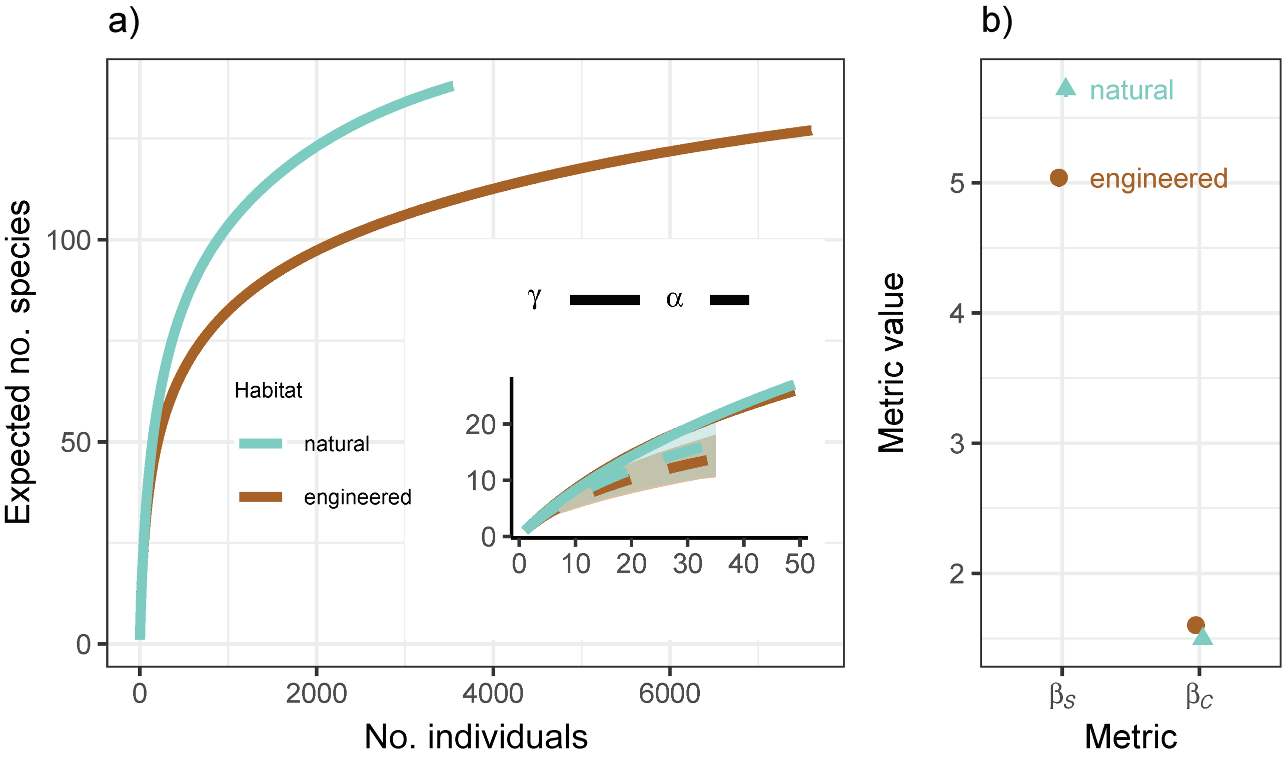

FIGURE 4 Total spatiotemporal β-diversity: (a) γ-scale rarefaction curves for each habitat, with inset showing γ- and average α-scales (note an individual α-scale curve was a single site in a single year); (b) mean β_S and β_C [point] (95% quantile whiskers not visible) of total spatiotemporal β-diversity jackknife resamples in each habitat type.

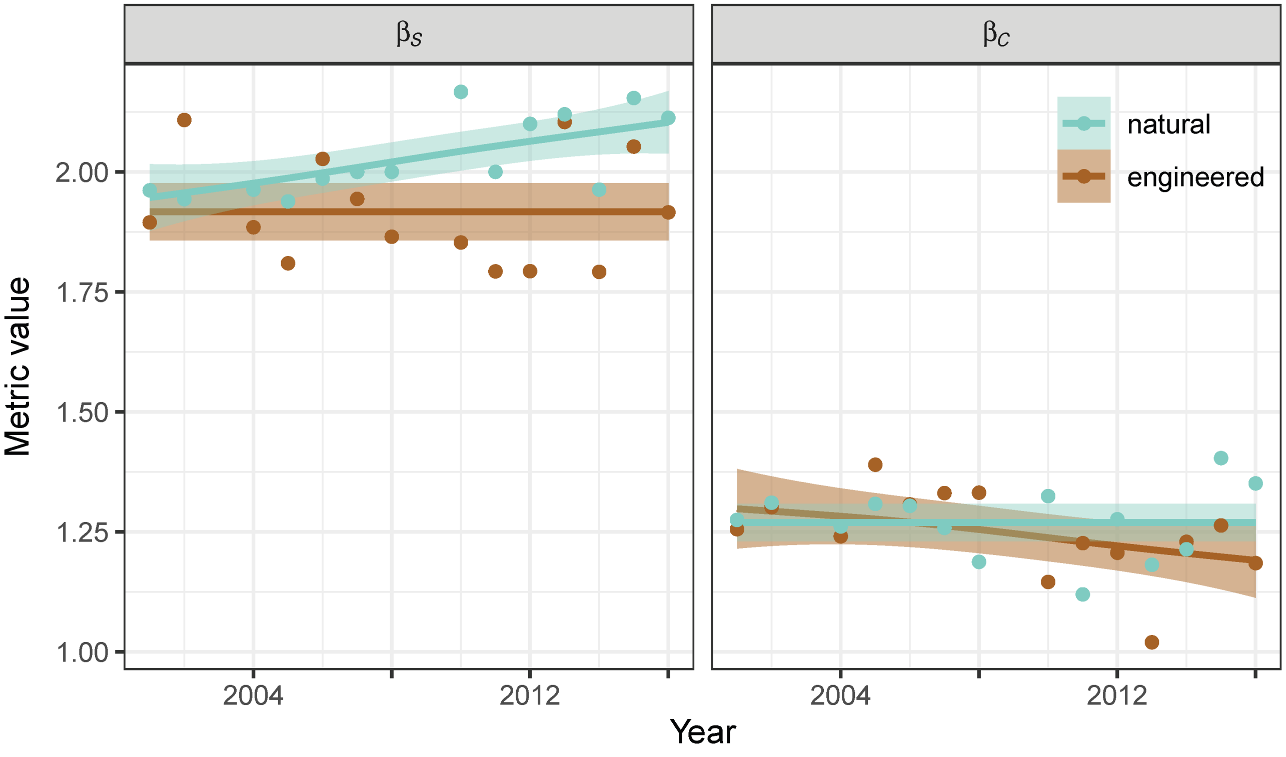

FIGURE 5 Spatial β-diversity as a function of time for β_S and β_C in the two habitats. Trend lines represent linear models with their 95% CI.

(Q3) Does the temporal variation in community composition differ between engineered and natural habitats?

Across all years, sites in the engineered habitat had greater variation than sites in the natural habitat in both the total number of individuals (i.e., the end points of the γ-scale curves on the *x*-axis, Figure 6a) and shape of the SAD (reflected by greater variation in the curvature of the γ-scale rarefaction). On average, natural sites had slightly higher levels of temporal β_S than the engineered sites, but the variation among sites (and only three replicates) meant there was no overall difference in temporal β_S between habitats (Figure 6b). We conclude that the weak differences in temporal β_S between habitats were primarily due to random sampling effects (Figure 6a) because this pattern disappeared for β_C (and β_C was slightly higher in the engineered habitat). In both habitats, β_S was also more than double the value of β_C, suggesting that more than 50% of year-to-year variation in community composition was due to changes in the number of individuals and/or rare species. Both habitats had similar β_C values, which indicated that the temporal autocorrelation of species presences was similar in the natural and engineered habitats.

(Q4) Are there compositional differences between engineered and natural habitats, and do any differences change through time?

Finally, the same concepts and tools that we used to examine variation in species composition within treatments can also be used to compare species composition between treatments through time. Essentially, this asks whether bird communities in natural and engineered sites are random subsets of a common larger species pool? Do nonrandom spatial patterns contribute to any differentiation? And do these patterns change over time? (Figure 7). Here, the overall difference between treatments (β_S) was larger than 1 (there is some species turnover between habitats) and slightly declined through time (homogenization). However, when only nonrandom patterns were considered, β_C was closer to, though still greater than 1, and only slightly declined through time. This suggests that once we control for sampling

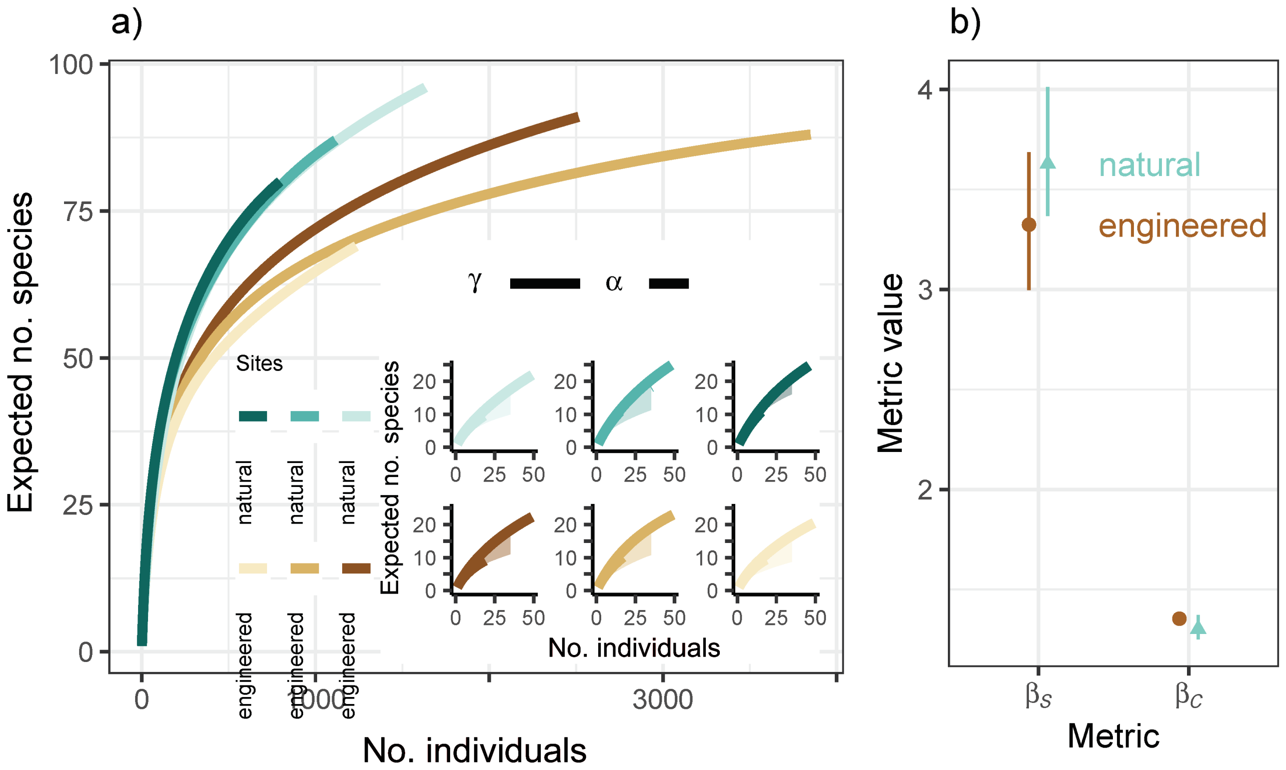

FIGURE 6 Temporal β-diversity: (a) γ-scale rarefaction curves for each site (i.e., all years combined), with inset showing γ- and the average α-scales for each site; (b) β_S and β_C (mean [point] and 95% quartiles [whiskers] of jackknife resamples) metrics of total temporal β-diversity.

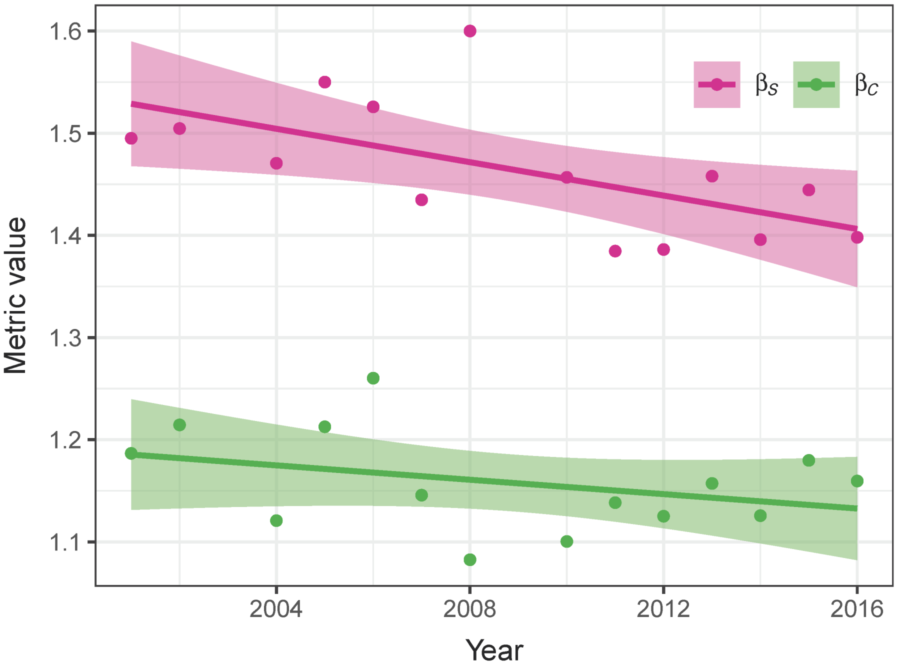

FIGURE 7 Spatial β-diversity metrics that measure the difference in species composition between the engineered and natural riparian habitat types as a function of time. Trend lines represent linear models with their 95% CI.

effects, compositional differences between the habitats were relatively small but still detectable and not changing through time.

DISCUSSION

We have described and demonstrated an integrated framework for quantifying the underlying causes of β-diversity and, namely, if those causes are due to random sampling effects or aggregating mechanisms such as environmental filtering and dispersal limitation. The approach that we have described provides a generalized framework for comparing patterns of total β-diversity, which we call β_S, to those that specifically partial out the nonrandom patterns of β-diversity (β_C). Using additional variables, such as environmental gradients or experimental treatments, it will be possible to judge which processes are ultimately responsible for nonrandom β-diversity detected using our approach. We have demonstrated that any question relating to how species composition changes across samples, whether they be taken through space or time, can be subject to the same approach and metrics. For many cases, this greatly simplifies what can seem a complex endeavor of finding the "right" β-metric for the question at hand.

Often, researchers switch β-diversity metrics and concepts when measuring compositional shifts within a meta-community or among heterogenous sites along an environmental gradient (e.g., Anderson et al., 2011). For example, within a meta-community, estimates of β-diversity are often based on measures of dispersion in community composition among sites (e.g., Anderson et al., 2006). These measures, however, can be strongly influenced by both the relative abundances of species and the size of the regional species pool. This means that randomization-based null models are needed if one wants to compare levels of dispersion among different meta-communities, and/or make inferences regarding potential driving mechanisms (e.g., Chase et al., 2011; Kraft et al., 2011; Myers et al., 2013). However, the appropriate form of randomization for the null model remains contentious (Kraft et al., 2012; Mori et al., 2015; Qian et al., 2012; Tucker et al., 2016; Xing & He, 2021). Our rarefaction-based approach can also be considered a type of null sampling model. However, comparing rarefaction curves has a number of benefits over other null model approaches: By calculating α- and γ-scale curves, β-diversity can be put back into the context of scale-dependent multicomponent changes in diversity (Blowes et al., 2022; Chase et al., 2018; Rolls et al., 2023); rarefaction curves can be based on analytical solutions improving efficiency; and rarefaction curves can be visualized, making them more intuitive and easier to communicate than other null model approaches. Nevertheless, some of the concerns arising from the use of null models also apply to the approach overviewed here. For example, there is a strong "Narcissus" effect (i.e., the outcome reflects the inputs) in developing null models to evaluate whether differences among samples deviate from a null expectation; the samples that are used to calculate γ-diversity influence the likelihood that they will deviate from a null expectation (Ulrich et al., 2017). The same is certainly true for the use of individual-based rarefaction curves in which deviations are mathematically constrained by the two end points of the rarefaction curve (McGlinn et al., 2019).

Baselga (2010) has advocated an approach that partitions measures of dissimilarity among samples (e.g., Jaccard's or Sorensen's index or an abundance-based equivalent) into measures that capture species turnover between samples, and those that account for the nestedness of species difference between samples (but see Šizling et al., 2022). In essence, the nestedness part of this partition is the same as our "random-placement" effect, while turnover captures the essence of our β-diversity measures that capture nonrandom variation among samples. For example, in our case study, we asked whether bird species in engineered and natural riparian habitats were a random subset of the same regional species pool (Figure 7). We found that β_S values were quite high compared with the β_C values, which indicates the turnover component is small relative to the nested component in Baselga's approach.

As with spatial β-diversity comparisons, there have been variable approaches to capture β-diversity through time (Legendre, 2019; Magurran et al., 2019; Tatsumi et al., 2022). Most measures of temporal turnover calculate turnover as a metric of community dissimilarity through time. Often rates of change between an initial and subsequent samples, or the rate of decay in dissimilarity as a function of the time elapsed between samples being compared are estimated, which can then be compared across systems or taxa (e.g., Blowes et al., 2019; Korhonen et al., 2010). However, as with spatial β-diversity, these measures cannot discern whether observed rates of turnover are different from what would be expected from a random placement model through time. Authors have used different approaches to remedy this problem. For example, Dornelas et al. (2014) compared rates of temporal β-diversity with those expected from a neutral model (Hubbell, 2001) to discern whether turnover rates were faster than expected under the assumption of neutral dynamics, while Stegen et al. (2013) used a null model to determine whether temporal turnover patterns were greater than expected from sampling effects. Temporal turnover can also be decomposed into changes due to abundances (similar to our "sampling" effects) and changes due to species turnover (Lamy et al., 2015; Shimadzu et al., 2015). As with spatial β-diversity measures, our approach is similar, but simplifies the problem by asking whether temporal changes are nonrandom in a time series.

Recently, authors have developed approaches to partition the influence of species gains and losses to changes in spatial β-diversity through time (Rosenblad & Sax, 2017; Tatsumi et al., 2021), and these have been expanded to incorporate changes in relative abundances (Tatsumi et al., 2022). These methods are useful for examining "winning" and "losing" species that underlie changes in spatial β-diversity through time. However, these methods risk isolating beta-diversity changes from local (α) and regional (γ) scale changes, and are unable to disentangle random versus nonrandom structure associated with these changes. Thus, our approach can provide a complementary, and more complete, picture into scale-dependent changes driving variation of spatial composition through time.

Finally, for simplicity we have focused here on two related metrics: β_S and β_C. Other measures of β diversity with different weights on common and rare species (i.e., Hill numbers) (Chao et al., 2012, 2023; Jost, 2007; Tuomisto, 2010; but see Lande, 1996) can also be calculated at different points along the rarefaction curves. For example, the metric based on Simpson's entropy, also known as the probability of interspecific encounter (PIE) (or Gini–Simpson index) (Hurlbert, 1971) (where $q = 2$ in the Hill number continuum; Chao et al., 2014; Jost, 2007), can be visualized as the slope at the base of the rarefaction curve (Chase et al., 2018; McGlinn et al., 2019). These Hill numbers or number equivalents can also be used with the multiplicative diversity partition used here (i.e., $\gamma = \alpha \times \beta$; Jost, 2007), and result in an effective number of distinct communities, with the tuning parameter (i.e., order q) determining the sensitivity to rare and common species. Recently, Chao et al. (2023) also proposed a framework for standardizing beta-diversity that considers the joint influence of sampling effects and spatial/temporal aggregation. Both their framework and ours standardize biodiversity data to the same level of sample coverage when comparing β between meta-communities. However, an important difference between the approaches is that Chao et al. (2023) assume that individuals are independently sampled (i.e., randomly encountered), whereas we assume that individuals within a sample are not independent of one another due to aggregation. In fact, our primary intention here is to explicitly quantify the important contributions of aggregation to β-diversity, which cannot be directly measured with the Chao et al. (2023) approach.

CONCLUSIONS

Ecologists are often interested in examining the role of meta-community-level mechanisms such as dispersal limitation and environmental filtering for patterns of β-diversity (Leibold & Chase, 2018; Vellend, 2016). The generalized approach that we have described relies on a set of intuitive metrics from sampling theory to quantify total β-diversity (β_S), and β-diversity due to nonrandom aggregation (β_C), which will allow for stronger tests of hypotheses related to mechanisms expected to influence patterns of aggregation. In addition, the framework provides an integrated way to examine how changes at finer (α) and coarser (γ) scales combine to determine variation in species composition (β). This places a central focus on scale-dependent diversity changes, with the potential to uncover deeper insights into scale dependence by varying the focal spatial or temporal grain of the analysis. It remains an open question as to how much variation in β-diversity reflects random sampling effects versus nonrandom aggregation effects. Our framework provides a means of addressing this question across space and time.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Code and data (McGlinn & Blowes, 2024; McGlinn et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.13914850; https://doi.org/10.5281/zenodo.13914830.

ORCID

Daniel J. McGlinn https://orcid.org/0000-0003-2359-3526
Shane A. Blowes https://orcid.org/0000-0001-6310-3670
Maria Dornelas https://orcid.org/0000-0003-2077-7055
Thore Engel https://orcid.org/0000-0002-9245-4397
Inês S. Martins https://orcid.org/0000-0003-4328-7286
Hideyasu Shimadzu https://orcid.org/0000-0003-0919-8829
Nicholas J. Gotelli https://orcid.org/0000-0002-5409-7456
Anne Magurran https://orcid.org/0000-0002-0036-2795
Brian J. McGill https://orcid.org/0000-0002-0850-1913
Jonathan M. Chase https://orcid.org/0000-0001-5580-4303

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