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Can additive beta-diversity be reliably partitioned into nestedness and turnover components?

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Running header: A warning on partitioning additive beta-diversity

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DATA ACCESSIBILITY

The incidence matrices and the R code used to run the analyses are provided in a GitHub repository (https://github.com/txm676/Partitioning-additive-beta). The repository has been archived on the Zenodo research data repository (DOI: 10.5281/zenodo.2595322).

BIOSKETCH

Tom Matthews is a macroecologist and biogeographer at the University of Birmingham, UK. He is interested in the application of macroecological methods to global environmental change questions, and his previous work has focused on the impacts of habitat fragmentation and the form of the species–area relationship in fragmented landscapes.

ABSTRACT

Aims: Quantifying β-diversity (differences in the composition of communities) is central to many ecological studies. There are many β-diversity metrics, falling mostly into two approaches: variance-based (e.g. the Sørensen index), or diversity partitioning (e.g. additive β-diversity). The former cannot be used when species–sites matrices are unavailable (which is often the case in island biogeography in particular) and only species richness data are provided. Recently, efforts have been made to partition additive β-diversity, a metric calculated using only α-diversity and γ-diversity, into nestedness and turnover components (termed here 'richness-only β-diversity partitioning'). We set out to test whether this form of β-diversity partitioning generates interpretable results, comparable with metrics based on species incidence β-diversity partitioning.

Location: Global

Time period: Present day

Major taxa studied: Multiple taxa

Methods: We first provide a brief review of β-diversity partitioning methods, with a particular focus on the development of richness-only β-diversity partitioning. Second, we use 254 empirical incidence matrices (provided with the paper) sourced from the literature to measure turnover and nestedness using incidence β-diversity partitioning, comparing the resulting values with those calculated using richness-only β-diversity.

Results: We provide an account of the emergence of β-diversity partitioning, with particular reference to the analysis of richness-only datasets and to the definition and usage of the relevant metrics. Analytically, we report weak correlations between turnover and nestedness calculated using the two different approaches. We show that this is because identical values of α-diversity and γ-diversity can correspond to incidence matrices with a range of different structures.

Main conclusions: Our results demonstrate that the use of richness-only β-diversity partitioning to measure turnover and nestedness is problematic and can produce patterns unrelated to conventional measures of turnover and nestedness. We therefore recommend that more accurate definitions are adopted for these terms in future studies.

INTRODUCTION

Quantifying differences in the composition of communities (i.e. measuring β-diversity) and testing the prevalence of nestedness in ecological communities are central to many ecological studies (Whittaker, 1960; Rosenzweig, 1995; Ulrich, Almeida-Neto, & Gotelli, 2009). Various metrics have been proposed to measure β-diversity (Koleff, Gaston, & Lennon, 2003; Tuomisto, 2010; Anderson et al., 2011; Chao, Chiu, & Hsieh, 2012) and many of these can be broadly divided into variance-based approaches (e.g. the Sørensen and Jaccard indices) and diversity partitioning-based approaches (Legendre & De Cáceres, 2013; Chao & Chiu, 2016). Recent work has bridged these two approaches to calculating β-diversity (Chao et al., 2012; Chao & Chiu, 2016). Nestedness, as originally conceived within island biogeography, refers to the ordered loss/gain of species along a richness gradient, whereby each larger assemblage tends to contain all the members of the previously considered site (Patterson & Atmar, 1986; Ulrich et al., 2009; Matthews, Cottee-Jones, & Whittaker, 2015). The calculation of most nestedness and variance-based β-diversity metrics requires knowledge of species occurrences at each site, coded in a binary presence-absence matrix (herein, incidence matrix), with species in rows and sites in columns (e.g. Legendre & Legendre, 1983; Koleff et al., 2003; Ulrich et al., 2009). Table 1 provides a glossary of the (many) different metrics discussed in the present study, and Fig. 1 provides an illustration of the different metrics.

Diversity partitioning and richness-only β-diversity partitioning: an overview

Over time, as research questions and meta-analytical tools have developed, the published literature has become an increasingly important source of data to extend the power of analyses via data mining. This is particularly true in regard to studies that conduct meta-analyses of β-diversity and nestedness (e.g. Cabral, Weigelt, Kissling, & Kreft, 2014; Matthews et al., 2015). However, in many cases the full incidence matrix for a set of sites is not available in previously published studies, and only the number of species in each site (α-diversity) and the regional diversity (γ-diversity) can be retrieved (e.g. Cowie, 1995). This is a particular problem in island biogeography, where several meta-analyses of ecological patterns on islands are based on these simple data (see, for example, various studies investigating species–area relationships (SAR), such as Triantis, Guilhaumon, & Whittaker, 2012; Matthews, Guilhaumon, Triantis, Borregaard, & Whittaker, 2016). Authors have attempted to get around this problem by estimating β-diversity and nestedness through diversity partitioning approaches (e.g. Chiarucci et al., 2010; Sfenthourakis & Panitsa, 2012; Cabral et al., 2014; see Zhang et al., 2014, for a terrestrial example).

Estimating β-diversity using diversity partitioning has a long history in ecology (Whittaker, 1960, 1965; MacArthur, Recher, & Cody, 1966; Lande, 1996; Jost, 2007; Tuomisto, 2010). The two main diversity partitioning approaches used are additive ($\beta_{Total} = \gamma - \alpha$), where β_{Total} is the amount by which regional diversity (γ) exceeds the mean diversity of a set of sites (α), and multiplicative ($\beta_{Mult} = \gamma / \alpha$), where β_{Mult} is the regional-to-local diversity ratio (Whittaker, 1960; Veech, Summerville, Crist, & Gering, 2002; Crist, Veech, Gering, & Summerville, 2003; Tuomisto 2010). Their relative merits have been much debated (see

Lande, 1996; Crist et al., 2003; Jost, 2007; Baselga, 2010a; Tuomisto, 2010; Veech & Crist, 2010), and recent work has shown how they (i.e. additive and multiplicative diversity partitioning) are mathematically linked (Chao et al., 2012). Additively partitioned β-diversity (β_{Total}), which is the focus of this present study, has been shown to be dependent on both γ and the number of sites (N), and it has thus been argued that β_{Total} should be normalised (by γ and N; β_{Stan}) in order to compare β-diversity values (Chao et al., 2012).

Using an additive partitioning approach, β_{Total} has been further partitioned into two sub-components, which have been argued to measure nestedness and turnover (we term this 'richness-only β-diversity partitioning'). This is different from the partitioning of dissimilarity indices (such as Sørensen and Jaccard indices), through analysis of an incidence matrix (we term this 'incidence β-diversity partitioning'), into turnover and nestedness-resultant dissimilarity / richness difference components (Baselga, 2010b, 2012; Carvalho, Cardoso, & Gomes, 2012). The use of richness-only β-diversity partitioning appears to have been based on the approach of Crist & Veech (2006), who used the power law SAR model to partition β_{Total} in isolated habitats into two components: β_{Area}, which is intended to describe how much of β_{Total} is due to the area effect, and β_{Replace}, which is intended to describe how much is explained by other factors (see Crist & Veech, 2006). β_{Area} is defined by Crist & Veech (2006, p.928) as "the mean deviation between the species richness of the largest habitat patch and the species richness of smaller patches". Subsequent studies have used the β_{Area} component as a measure of nestedness, and the β_{Replace} component as a measure of replacement/turnover (e.g. Chiarucci et al., 2010; Sfenthourakis & Panitsa, 2012; Cabral et al., 2014; Zhang et al., 2014). It is important to note that the interpretation of β_{Area} and β_{Replace} as measures of nestedness and turnover, respectively, was not necessarily implied in the original study (Crist & Veech, 2006), a fact recognised by at least one of the subsequent studies (Cabral et al., 2014).

To take one study that used richness-only β-diversity partitioning as an example, Chiarucci et al. (2010, p.86), in their study of plants on a variety of Macaronesian islands, use the term $\beta_{\text{Nestedness}}$ (rather than β_{Area}), stating that "the first component of [additive] β-diversity ($\beta_{\text{Nestedness}}$) quantified the degree of nestedness of the flora," whilst the "second β component ($\beta_{\text{Replacement}}$) measure[s] the differences in species composition among the flora of the islands within an archipelago, and [is] a measure of the compositional differences across islands." The authors then proceed to make inferences regarding the nestedness of their data; for example, "the higher importance of $\beta_{\text{Nestedness}}$ for pteridophytes indicated that, for this taxon, the flora of each island is largely formed by a subset of species that make up the archipelago flora" (Chiarucci et al., 2010, p. 89). This example, and others (e.g. Sfenthourakis & Panitsa, 2012; Cabral et al., 2014; Zhang et al., 2014), illustrates that colleagues have started to use richness-only β-diversity partitioning in their research; the use of the method and its implications is not confined to those four cited studies and a simple Google Scholar search indicates these four papers have been cited over 80 times. It is therefore timely to assess the implications of this approach and how well the richness-only β-diversity partitions correspond with conventional measures of nestedness and turnover, as this could constitute a useful analytical tool if it can be shown to be robust.

In this article, we use a dataset of 254 incidence matrices (details below) to assess to what extent nestedness and turnover calculated by richness-only β-diversity partitioning (i.e. partitioning additive β-diversity, i.e. β_{Total}) are congruent with nestedness and compositional difference metrics calculated using the full incidence matrix. It is important to re-stress that we are focused on the issues surrounding the use of richness-only β-diversity partitioning (i.e. when there is no incidence matrix and thus no information on which species are present on which island; e.g. as employed by Chiarucci et al., 2010), and not incidence β-diversity partitioning (e.g. the partitioning of Sørensen dissimilarity; e.g. Baselga, 2012). As β_{Total} is known to be problematic due to its dependency on both γ and the number of sites (N), we might expect the partitioned components of β_{Total} to also have issues. However, this possibility has not previously been explored, and it is important that any problems with the approach are highlighted to avoid the proliferation of incorrect metrics (or at least the incorrect interpretation of particular metrics) in the ecological literature.

MATERIALS AND METHODS

To compare nestedness and turnover calculated using richness-only β-diversity partitioning (i.e. additive partitioning of β_{Total}) with nestedness and compositional difference metrics based on incidence β-diversity partitioning (i.e. analysis of the full incidence matrix), we used a collection of island incidence matrices that we sourced from the literature. Briefly, the database contains 254 incidence matrices of various taxa from different island systems (each representing a geographically coherent set of islands), including all major island types such as volcanic oceanic islands, continental-shelf islands, atolls, and habitat islands. Unlike other collections of incidence matrices (e.g. Atmar & Patterson, 1995; Strona, Ulrich, & Gotelli, 2017), our database is comprised solely of island datasets and thus allows us to make general conclusions regarding patterns of interest in islands (Whittaker & Fernández-Palacios, 2007; Matthews, 2015). The full database will be published as part of a separate upcoming study, but the set of 254 incidence matrices are available from GitHub (txm676/ Partitioning-additive-beta). The repository has been archived on the Zenodo research data repository (DOI: 10.5281/zenodo.2595322).

For each of the 254 datasets, we calculated additive β-diversity (β_{Total}). Thus, the incidence matrices were not used; we simply used mean α (the average richness of the set of islands in a dataset) and γ (the overall species richness of the set of islands in a dataset). We also calculated normalised β-diversity (β_{Stan}) using the approach in Chao et al. (2012):

$$\beta_{Stan} = \frac{\beta\text{Total}}{(1-\frac{1}{\text{N}})\gamma},$$

where N is the number of islands. We then calculated the $\beta_{\text{Nestedness}}$ and $\beta_{\text{Replacement}}$ (Table 1) partitions of β_{Total} (i.e. richness-only β-diversity partitioning) using the approach of Chiarucci et al. (2010). This approach differs slightly from that employed by Crist & Veech (2006) in that it uses the maximum observed richness of an island in the dataset rather than maximum richness predicted by the power law SAR model. However, the two approaches produce highly correlated values (Spearman's rho = 0.88, $P<0.001$, for the correlation between the $\beta_{\text{Nestedness}}$ of Chiarucci et al. (2010) and the β_{Area} of Crist and Veech (2006) based on the 254 empirical matrices). Following Chiarucci et al. (2010) $\beta_{\text{Nestedness}}$ was calculated using the equation:

$$\beta_{Nestedness} = \frac{1}{N}\sum_{i=1}^{N}(S_{max} - S_i), \tag{1}$$

where S_i is the number of species on the i-th island, and S_{max} is the number of species on the most species rich island. $\beta_{\text{Replacement}}$ can then be calculated using the equation:

$$\beta_{Replacement} = \beta_{Total} - \beta_{Nestedness}. \tag{2}$$

We note that eq. 1 can be reformulated to clarify the meaning of $\beta_{\text{Nestedness}}$:

$$\beta_{Nestedness} = \frac{1}{N}\sum_{i=1}^{N}(S_{max} - S_i) = S_{max} - \frac{1}{N}\sum_{i=1}^{N} S_i = S_{max} - \alpha. \tag{3}$$

This is in accordance with the initial definition of β_{Area} by Crist & Veech (2006). As the average local diversity, α, is independent of the number of sites considered $\beta_{\text{Nestedness}}$ can be derived from the knowledge of two sites having S_{max} and S_r species,

$$\beta_{Nestedness} = S_{max} - \frac{S_{max}+S_r}{2} = \frac{S_{max}-S_r}{2}, \tag{4}$$

Therefore, $\beta_{\mathrm{Nestedness}}$ reduces to a difference in species richness between two sites, irrespective of the occurrence of joint species among these sites. This contradicts the basic definition of nestedness, which asserts the existence of an ordered set of subsamples (Patterson & Atmar, 1986; Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008). Taking the extreme case of there being no shared species, and thus with the maximum possible species turnover, $\beta_{\mathrm{Nestedness}}$ can take any of the full range of possible values between zero and $S_{\mathrm{max}} - \alpha$.

We also measured the compositional difference between islands in a dataset using the Sørensen dissimilarity index computed on the full incidence matrix, using the 'betapart' R package (version 1.4-1, Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2017). Overall compositional difference was calculated using Sørensen multi-site dissimilarity ($\beta_{\mathrm{Sor;}}$ see Table 1),

$$\beta_{\mathrm{Sor}} = \frac{\left[\sum_{i<j} \min(b_{\mathrm{ij}}, b_{\mathrm{ji}})\right] + \left[\sum_{i<j} \max(b_{\mathrm{ij}}, b_{\mathrm{ji}})\right]}{2\left[\sum_{i} S_{\mathrm{i}} - S_{\mathrm{T}}\right] + \left[\sum_{i<j} \min(b_{\mathrm{ij}}, b_{\mathrm{ji}})\right] + \left[\sum_{i<j} \max(b_{\mathrm{ij}}, b_{\mathrm{ji}})\right]} \qquad (5)$$

where S_{i} is the total number of species in site i, S_{T} is the total number of species in all sites considered together and b_{ij}, b_{ji} are the number of species exclusive to sites i and j, respectively. Sørensen multi-site dissimilarity was partitioned (i.e. incidence β-diversity partitioning) into the turnover component (Simpson multi-site dissimilarity; β_{Sim}; see Table 1),

$$\beta_{\mathrm{Sim}} = \frac{\left[\sum_{i<j} \min(b_{\mathrm{ij}}, b_{\mathrm{ji}})\right]}{\left[\sum_{i} S_{\mathrm{i}} - S_{\mathrm{T}}\right] + \left[\sum_{i<j} \min(b_{\mathrm{ij}}, b_{\mathrm{ji}})\right]} \qquad (6)$$

and the nestedness component (Nestedness-resultant multi-site dissimilarity; β_{Sne}, Baselga, 2010b, 2012),

$$\beta_{Sne} = \frac{\left[\sum_{i<j}\max(b_{ij}, b_{ji})\right] - \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]}{2\left[\sum_{i} S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right] + \left[\sum_{i<j}\max(b_{ij}, b_{ji})\right]} * \frac{\sum_{i} S_i - S_T}{\left[\sum_{i} S_i - S_T\right] + \left[\sum_{i<j}\min(b_{ij}, b_{ji})\right]} \qquad (7)$$

As β_{Sne} is conceptually distinct from 'true' nestedness (Almeida-Neto, Frensel, & Ulrich, 2012; Baselga 2012), we also measured the nestedness of each dataset with the NODF ('nestedness metric based on overlap and decreasing fill') metric (Almeida-Neto et al., 2008). According to NODF, an incidence matrix sorted in decreasing order of marginal totals is maximally nested when there is complete overlap of presence values (1s) from the right to the left column and from the bottom to the top row, and no ties in both the row and column marginal totals. We chose NODF as it is widely considered to be the most appropriate measure of nestedness (Ulrich et al., 2009). NODF was computed on the full incidence matrix, using the vegan R package (version 2.4-5, Oksanen et al., 2017). We used a combination of graphical plots and Kendall rank correlation tests to assess the correlation between the richness-only β-diversity partitioning metrics, $\beta_{Nestedness}$ and $\beta_{Replacement}$, and the incidence β-diversity partitioning metrics, β_{Sim} and β_{Sne}, and also NODF. We used the Kendall rank correlation test rather than Spearman rank correlations as the former is argued to provide better results with small sample sizes. To illustrate that the issues we highlight lie with richness-only β-diversity partitioning and not with additive β-diversity (β_{Total}) itself, we also assessed the correlation between β_{Stan} and β_{Sor} using a Kendall rank correlation test.

To determine whether our results were consistent across different types of island datasets, we divided our main dataset a number of different ways. First, we split the datasets into true islands (oceanic and continental-shelf islands, and islands within natural lakes) and habitat islands (all other datasets). Second, we calculated the quantiles, using all datasets, of each of: the number of islands, α, and γ. For each factor, we then took the datasets representing the top and bottom quantiles (lowest and highest 25%) to be individual subsets. We then repeated the above analyses using each individual subset. Finally, we repeated the main correlation tests using the multisite version of Jaccard dissimilarity calculated using both the Baselga (2012) and the Carvalho et al. (2012) approaches. The above analyses were undertaken using the R programming language (Version 3.5.2, R Core Team, 2017), and the R code used to run the analyses is provided in a GitHub repository (txm676/ Partitioning-additive-beta).

RESULTS

Considering the full set of 254 empirical island incidence matrices, we found low (often very low) correlation between the relevant metrics. The lowest correlation was between $\beta_{\mathrm{Nestedness}}$ and β_{Sne} (Kendall's tau = -0.04; *P*-value = 0.36), followed by $\beta_{\mathrm{Nestedness}}$ and NODF (Kendall's tau = -0.11; *P*-value = 0.01), $\beta_{\mathrm{Replacement}}$ and β_{Sor} (Kendall's tau = 0.23; *P*-value < 0.001) and $\beta_{\mathrm{Replacement}}$ and β_{Sim} (Kendall's tau = 0.43; *P*-value < 0.001). As expected, there was a higher correlation between β_{Stan} and β_{Sor} (Kendall's tau = 0.56; *P*-value < 0.001). The plots of these relationships are provided in Figure 2; certain variables were logged prior to plotting (but not analysis) to ease the visual interpretation (see the legend of Figure 2). A complete set of pairwise scatter plots (along with their correlations) for all variables is provided as Figure S1 in Appendix S1.

Re-running the analyses using the different dataset subsets generated broadly similar results (Table S1 in Appendix S1). The main difference was for the correlation between $\beta_{\mathrm{Nestedness}}$ and β_{Sne}, whereby for three subsets ($\alpha > 25$, $\gamma < 20$ and $\gamma > 77$) the correlation was positive and significant, although the correlation coefficient was less than 0.50 in all three cases (Table S1). The results of the analyses using the multisite version of Jaccard dissimilarity calculated using both the Baselga (2012) and the Carvalho et al. (2012) approaches were similar to the main results and are not discussed further (Appendix S1).

DISCUSSION

We have explored to what extent nestedness and turnover calculated through richness-only β-diversity partitioning (i.e. partitioning β_{Total}) are congruent with nestedness and compositional difference metrics calculated using incidence β-diversity partitioning. We find that neither partition of β_{Total} provides good measures of what is commonly regarded as nestedness or turnover. Our results lead us to caution the interpretation of the additive sub-components of β_{Total} as metrics of nestedness and replacement/turnover. The problem is most acute when considering nestedness: $\beta_{Nestedness}$ and NODF calculated using the empirical matrices were in fact weakly negatively correlated (tau = -0.11). A thought experiment that further illustrates the issue with $\beta_{Nestedness}$ is provided in Appendix S2. Thus, $\beta_{Nestedness}$ should simply be interpreted as representing area effects, as originally proposed by Crist & Veech (2006). Based on analyses of the empirical matrices, the correlation between $\beta_{Replacement}$ and β_{Sim} was also low (tau = 0.43) and we do not recommend using $\beta_{Replacement}$ in future studies to measure turnover. This is likely due to the fact that $\beta_{Replacement}$ is not normalised (by either N or γ). Rather, dissimilarity measures should be preferred when the full incidence matrix is available (Roden et al., 2018), and β_{Stan} or an equivalent metric (see Chao et al., 2012; Chao & Chiu, 2016) should be used when it is not available.

Partitioning methods based on only γ and α-diversity (i.e. richness-only β-diversity partitioning) intrinsically disregard the species composition of each site which, depending on the structure of the underlying incidence matrix, may have a disproportionate effect on the accuracy of partitioned measures. This is rather intuitive: for a given combination of γ and α-diversity values, one can generate a very large number of different matrices, due to the fact that neither γ nor α include information on the number of sites in the system. However, even if we fix the number of sites to a given value N (in reality the number of islands in an archipelago should be known), the number of matrices with γ species, N sites and average species richness per site equal to α might still be very large. In turn, this means that a given partitioned measure of β-diversity or nestedness may potentially correspond to a broad array of different values of their matrix-wide counterparts. To illustrate this concept, we chose a random block of 20 matrices from the set of 254 incidence matrices used in the main analysis, and we used a simple procedure to explore how much, for each matrix, we could modify the matrix structure towards either higher or lower β-diversity and nestedness relative to the observed values, without altering γ, α or N (see Appendix S3 for details). For clarity, results for a subset of five matrices are reported in Figure 3, whilst we provide separate plots for each of the 20 matrices in Figure S2 in Appendix S3. As expected, for a given matrix, the same γ, α and N can result in a wide range of internal matrix structure, especially in terms of nestedness. In turn, this makes it very difficult to draw parallels between the matrix-wide and the partitioned concepts of turnover and nestedness, as the latter might span a very large spectrum of cases that can only be finely discriminated using the former.

The results of our main analyses were largely consistent for the different subsets of datasets, although there were a few subsets ($\alpha > 25$, $\gamma < 20$ and $\gamma > 77$) for which the correlation between $\beta_{\mathrm{Nestedness}}$ and β_{Sne}, was positive and significant. In datasets with low γ, the richness differences between islands are likely constrained and thus $\beta_{\mathrm{Nestedness}}$ and β_{Sne} are both restricted to low values, which could explain the positive correlation between $\beta_{\mathrm{Nestedness}}$ and β_{Sne} for the low γ subset. The reason for the positive correlations observed in the high γ and high α subsets is unclear, but may point towards a joint dependency between the metrics and γ. That being said, it should be noted that, whilst the correlations were significant, the coefficients were relatively low (i.e. 0.23, 0.24 and 0.44) and thus our ability to make conclusions based on these results is limited.

The results of the present study clearly illustrate the issues with using richness-only β-diversity partitioning to measure species turnover and nestedness, and we recommend that, if using this approach, more accurate definitions are adopted for these terms in future studies. Readers are directed to Ulrich et al. (2009), Baselga (2012) and Chao & Chiu (2016) for discussion of other nestedness and β-diversity metrics. Perhaps more generally, the results of this study also highlight the benefits of the deposition of datasets from published studies in data archives.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at …

TABLES

Table 1. A glossary of the different β-diversity and nestedness metrics used in this study. The metrics are split into those that are calculated using the incidence matrix and those that are calculated using simple richness data (i.e. γ and α-diversity).

Metric	Description	References
	Incidence Matrix Metrics	
β_{Sor}	Sørensen dissimilarity; a β-diversity metric that measures compositional differences between sites.	Baselga (2010, 2012)
β_{Sim}	Simpson dissimilarity; the turnover component of Sørensen dissimilarity.	Baselga (2010, 2012)
β_{Sne}	Nestedness-resultant fraction of Sørensen dissimilarity.	Baselga (2010, 2012)
NODF	A nestedness index based on the twin properties of standardized differences in matrix row and column fills and paired overlap.	Almeida-Neto et al. (2008)
	Richness-Only Metrics	
β_{Total}	β-diversity calculated using additive diversity partitioning; the amount that regional diversity exceeds the mean diversity of a set of sites.	MacArthur et al. (1966), Lande (1996), Veech et al. (2002)
β_{Stan}	β_{Total} normalised by γ and the number of sites.	Chao et al. (2012)
$\beta_{Nestedness}$	Hitherto interpreted as a measure of nestedness. Its calculation is almost identical to the β_{Area} metric of Crist and Veech (2006) but uses the maximum observed richness of an island in the dataset rather than maximum richness predicted by the power law SAR model.	Chiarucci et al. (2010), Cabral et al. (2014), Zhang et al. (2014)
$\beta_{Replacement}$	The turnover component of $\beta_{Total.}$ Hitherto interpreted as a measure of the compositional differences across a set of sites. Similar in calculation to the $\beta_{Replace}$ of Crist and Veech (2006).	Chiarucci et al. (2010), Cabral et al. (2014), Zhang et al. (2014)
β_{Area}	Measures the portion of β_{Total} that is due to area effects.	Crist & Veech (2006)
$\beta_{Replace}$	The portion of β_{Total} that is due to factors other than area.	Crist & Veech (2006)
β_{Mult}	β-diversity calculated using multiplicative diversity partitioning; the regional-to-local diversity ratio (true β-diversity).	Whittaker (1960, 1965), Jost (2007), Tuomisto (2010)

FIGURES

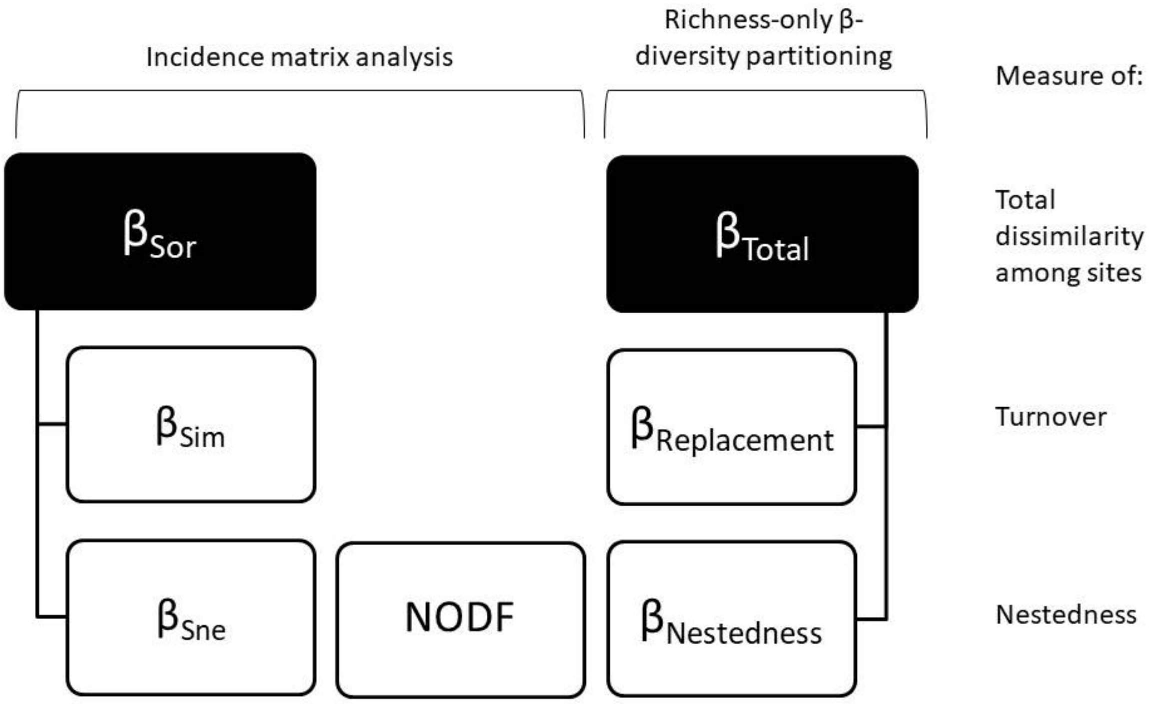

Figure 1. Overview of the various total β-diversity, turnover and nestedness metrics discussed in the main text. The metrics are organised within the figure according to how they are calculated (richness-only β-diversity partitioning and incidence matrix analysis), and to what it is they are purported to be measuring (total β-diversity, turnover or nestedness). The two solid black boxes indicate metrics that have been partitioned into two components (connected by the black lines). Here, richness-only β-diversity partitioning relates to the partitioning of additive β-diversity. For definitions of terms, see Table 1.

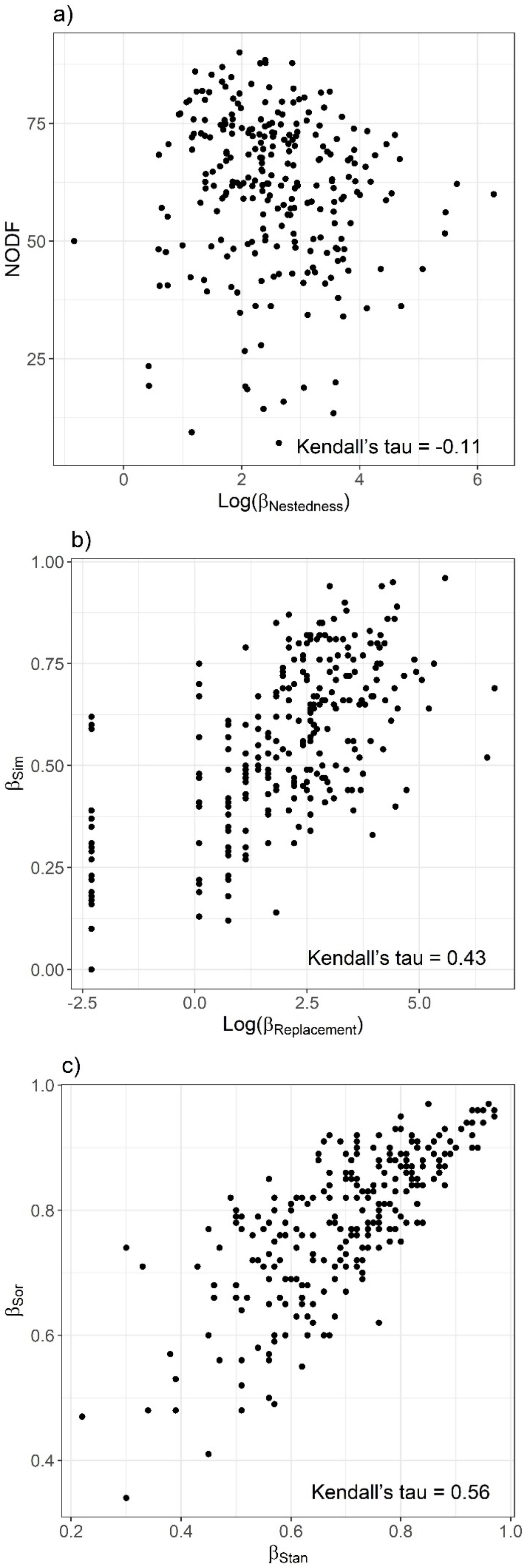

Figure 2. Scatter plots showing the relationship between different β-diversity and nestedness metrics, calculated using richness-only β-diversity partitioning and through analysing the full incidence matrix. The data are 254 empirical incidence matrices from different island systems (e.g. oceanic islands, habitat islands). The metrics on the x-axis in all three plots are those calculated using richness-only β-diversity partitioning, whereas those on the y-axis were calculated using the full incidence matrix. For the definitions of the variables, see Table 1. $\beta_{Nestedness}$ and $\beta_{Replacement}$ have been logged (base-e; a constant of 0.1 was added to all values to avoid zero values) for presentation purposes.

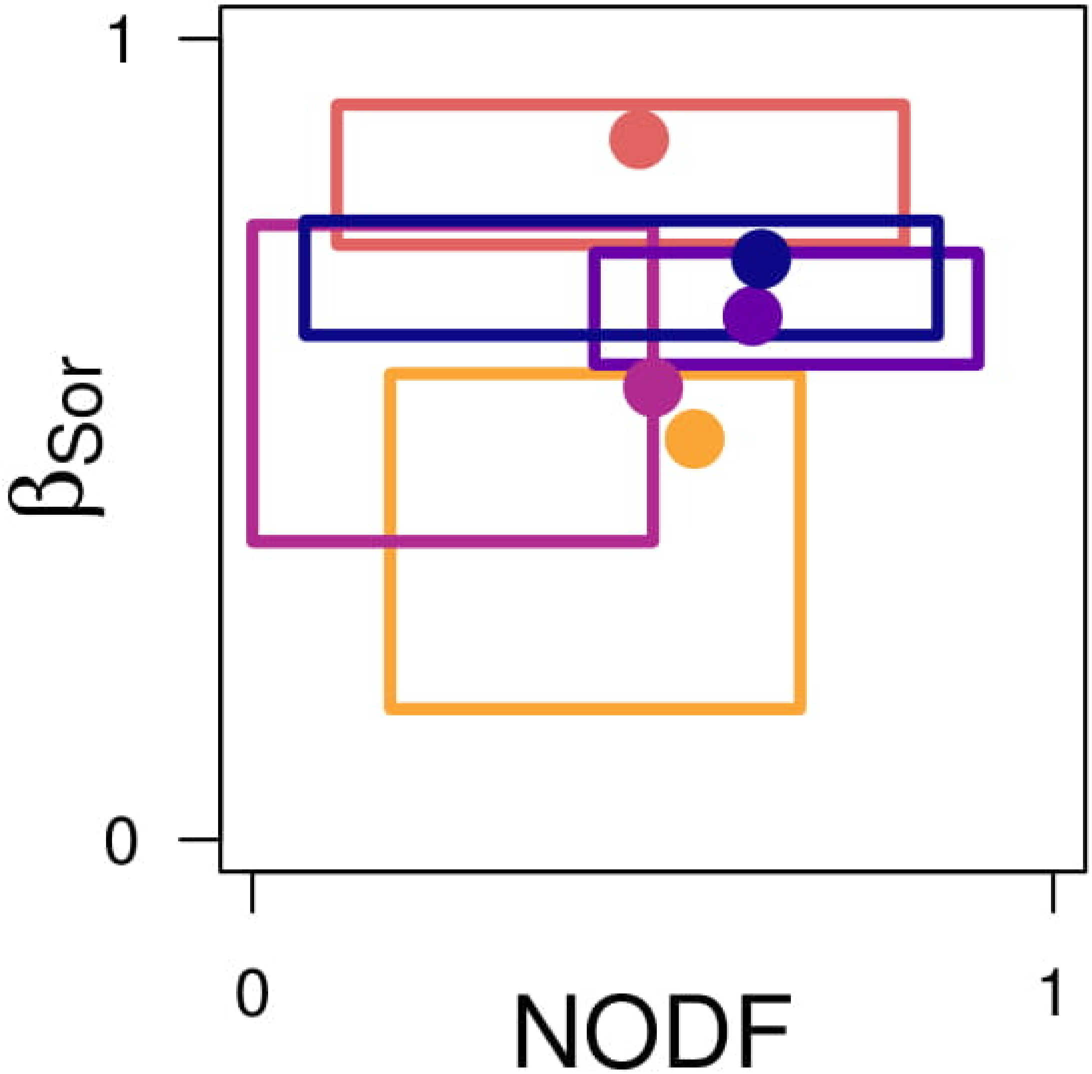

Figure 3. The range of possible NODF and β_{Sor} values for five incidence matrices, given the constraints of a dataset's γ-diversity, α-diversity and number of islands. For a given matrix the coloured rectangle represents the range of possible values, and the same coloured dot represents the observed values for that matrix. In each case, the procedure consisted of attempting a large number of random swaps (10, 000) between species presences / absences within sites, retaining only those swaps that moved the matrix structure in the desired direction (i.e. towards the extremes of possible NODF and β_{Sor} values). Five incidence matrices were randomly selected from the full set of 254.