MACROECOLOGICAL METHODS

The relationship between species replacement, dissimilarity derived from nestedness, and nestedness

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ABSTRACT

Aim Beta diversity can be partitioned into two components: dissimilarity due to species replacement and dissimilarity due to nestedness (Baselga, 2010, *Global Ecology and Biogeography*, **19**, 134–143). Several contributions have challenged this approach or proposed alternative frameworks. Here, I review the concepts and methods used in these recent contributions, with the aim of clarifying: (1) the rationale behind the partitioning of beta diversity into species replacement and nestedness-resultant dissimilarity, (2) how, based on this rationale, numerators and denominators of indices have to match, and (3) how nestedness and nestedness-resultant dissimilarity are related but different concepts.

Innovation The rationale behind measures of species replacement (turnover) dictates that the number of species that are replaced between sites (numerator of the index) has to be relativized with respect to the total number of species that could potentially be replaced (denominator). However, a recently proposed partition of Jaccard dissimilarity fails to do this. In consequence, this partition underestimates the contribution of species replacement and overestimates the contribution of richness differences to total dissimilarity. I show how Jaccard dissimilarity can be partitioned into meaningful turnover and nestedness components, and extend these new indices to multiple-site situations. Finally the concepts of nestedness and nestedness-resultant dissimilarity are discussed.

Main conclusions Nestedness should be assessed using consistent measures that depend both on paired overlap and matrix filling, e.g. NODF, whereas beta-diversity patterns should be examined using measures that allow the total dissimilarity to be separated into the components of dissimilarity due to species replacement and dissimilarity due to nestedness. In the case of multiple-site dissimilarity patterns, averaged pairwise indices should never be used because the mean of the pairwise values is unable to accurately reflect the multiple-site attributes of dissimilarity.

Keywords

Beta diversity, dissimilarity, nestedness, richness differences, spatial turnover, species replacement.

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INTRODUCTION

The term beta diversity was first introduced by Whittaker (1960). However, the use of similarity or dissimilarity measures to analyse patterns of variation in species composition is in fact much older (e.g. Jaccard, 1912; Simpson, 1943). The strict sense definition of beta diversity is the ratio between gamma and mean alpha diversities (Tuomisto, 2010), i.e. the factor to which the diversity of a region exceeds the mean diversity of local sites

within the region. It is clear that gamma diversity can be different from mean alpha diversity if, and only if, local sites differ in species composition. Therefore, the actual parameter determining the ratio between gamma and mean alpha diversities is the degree to which species composition changes from site to site. For this reason, the term beta diversity is usually applied in a broad sense to any measure of variation in species composition (Anderson *et al.*, 2011). In fact, some of the most popular measures of variation in species composition, like the Jaccard and

Sørensen indices, are monotonic transformations of beta diversity that therefore reflect the same concept (Jost, 2007).

Although the intuitive concept of 'change in species composition' is apparently straightforward, two different phenomena can produce differences in species composition between two sites. The first phenomenon is the replacement of some species by others from site to site, a concept that has been termed spatial turnover (Gaston & Blackburn, 2000). The second phenomenon is nestedness, a pattern characterized by the poorest site being a strict subset of the richest site. In this case both sites have obviously different species composition (i.e. the richest site has unique species not present in the poorest site), but no species is replaced by other. This effect of richness differences in measures of compositional change was realized by Simpson (1943) as he noted that richness differences could be responsible for the dissimilarity between sites even in the absence of species replacement. His important observation had generally been neglected until it was reintroduced by Lennon *et al.* (2001). Independently, several other authors have also highlighted the relationship between beta diversity and nestedness. For example, Harrison *et al.* (1992) stressed that Whittaker's beta diversity 'does not distinguish between true species turnover along a distance (or environmental) gradient, and situations in which species drop out along the gradient without any new species being added'. Several years later Williams (1996) suggested the use of 'non-nestedness' as a measure of spatial turnover. My work stems from these contributions and has shown (Baselga, 2010) that the total dissimilarity between two assemblages (i.e. beta diversity or, in my specific framework, a monotonic transformation of beta diversity – Sørensen dissimilarity, β_{sor}) can be partitioned into two components: dissimilarity due to species replacement (Simpson dissimilarity or spatial turnover, β_{sim}) and dissimilarity due to nestedness (nestedness-resultant dissimilarity, β_{nes}). It should be noted that the second component is not a measure of nestedness itself, but a measure of the fraction of total dissimilarity that it is not caused by species replacement but instead by nestedness.

Using this additive partitioning of dissimilarity, subsequent contributions have successfully shown that the turnover and nestedness components of beta diversity have contrasting spatial patterns and that the separation of these components is crucial for understanding the historic and present-day determinants of beta diversity (e.g. Dobrovolski *et al.*, 2012; Hortal *et al.*, 2011; Leprieur *et al.*, 2011; Svenning *et al.*, 2011). However, three recent papers have criticized this framework for partitioning beta diversity and/or have proposed alternative approaches. I will discuss these comments in order of their chronological appearance online. The first contribution (Podani & Schmera, 2011, hereafter referred to as PS for brevity), argues for a new approach to combine several measures of beta diversity, nestedness and richness differences. The second paper (Carvalho *et al.*, 2012, hereafter referred to as CCG) argues for an alternative approach for partitioning the total dissimilarity into two different components supposed to account for species replacement and richness differences. As I will show below, the approaches taken in these two papers are tightly related, and therefore share

identical problems. Finally, a third contribution (Almeida-Neto *et al.*, 2012, hereafter referred to as AFU) argues that the pairwise and multiple-site measures of the nestedness component of beta diversity (β_{nes} and β_{NES}) are not true measures of the nestedness-resultant dissimilarity between sites, and that this should be quantified using a measure of nestedness.

The aim of this paper is to review all the concepts and methods used in these recent contributions, clarifying (1) the rationale behind the partitioning of beta diversity into species replacement and nestedness-resultant dissimilarity, (2) how, based on this rationale, numerators and denominators of indices have to match to build meaningful measures, and (3) how nestedness and dissimilarity derived from nestedness are related but different concepts.

THE RELATIONSHIP BETWEEN PS AND CCG FRAMEWORKS

The whole framework proposed by PS relies on a simple decomposition of the total number of species (n, gamma diversity) for a pair of sites:

$$n = a + b + c \tag{1}$$

where a is the number of species present in both sites, b is the number of species present in the first site but not in the second, and c is the number of species present in the second site but not in the first. After some simple rearrangements, they show:

$$n = a + b + c = a + 2\min(b,c) + |b - c| \tag{2}$$

and, dividing all terms by n, 'in order to make the calculations independent of total species richness':

$$1 = a/n + 2\min(b,c)/n + |b - c|/n \tag{3}$$

Using different combinations of these three terms, PS propose several measures. For example, $\beta_{rel} = 2\min(b,c)/n + |b - c|/n$ is in fact the well-known Jaccard index of dissimilarity ($b + c/n$). Although PS use the acronym β_{rel}, I find it clearer not to multiply terms and use β_{jac} for simplicity. Therefore, PS propose that the Jaccard dissimilarity (accounting for beta diversity) can be decomposed into two components:

$$\beta_{jac} = \frac{b+c}{a+b+c} = \frac{2\min(b,c)}{a+b+c} + \frac{|b-c|}{a+b+c}. \tag{4}$$

In the opinion of PS, the first component ($R_{rel} = 2\min(b,c)/n$) would account for species replacement and the second ($D_{rel} = |b - c|/n$) would account for richness differences. Another combination of terms, $N_{rel} = a/n + |b - c|/n$, $a > 0$, is proposed by PS as a measure of nestedness.

A similar approach for partitioning Jaccard dissimilarity into the same two additive components was independently proposed by CCG. Although CCG use the acronym β_{cc} to refer to Jaccard dissimilarity, I use β_{jac} hereafter for simplicity. Thus, the CCG partition is $\beta_{jac} = \beta_{-3} + \beta_{rich}$ which is algebraically straightforward
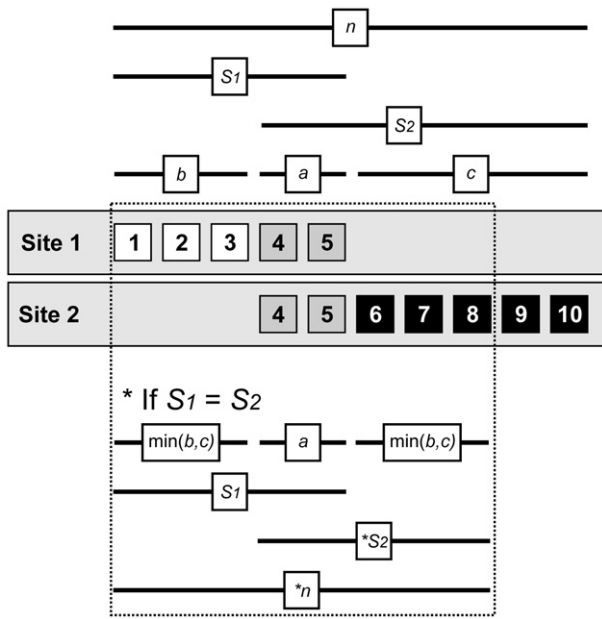
Figure 1 Schematic representation of the species counts involving two sites: the total number of species (n), the richness of each site (S_1 and S_2), the number of species present in both sites (a) and the number of species exclusive to each site (b and c, respectively). In the absence of richness differences (dotted square), these quantities would be different, as shown below: the number of exclusive species would be $\min(b,c)$ in each site [that is $2\min(b,c)$ in total], so the sum of the richness of both sites would be $2a + 2\min(b,c)$ and the total number of species would be $a + 2\min(b,c)$.

as shown above, because $R_{rel} = \beta_{-3}$ and $D_{rel} = \beta_{rich}$. Thus, the CCG and PS approaches for decomposing beta diversity are identical.

REPLACEMENT MEASURES: MISCONCEPTION AND SOLUTION

However, what PS and CCG have not proved is whether these additive components account for the ecological concepts they are intending to measure. In fact, the simple theoretical example shown by CCG (Carvalho *et al.*, 2012; Fig. 1 and Table 1) suggests the opposite: the replacement component β_{-3} ($= R_{rel}$) is exactly the same for a pair of sites that do not share any species (sites A–F in CCG) as for a pair of sites with almost all species in common (sites A and B in CCG). This behaviour is inconsistent with a measure of species replacement, i.e. spatial turnover in the terminology used by Baselga (2010), based on Harrison *et al.* (1992), Williams (1996) and Gaston & Blackburn (2000). The problem with the PS and CCG approaches arises from the fact that the denominator of β_{-3} ($= R_{rel}$) is not the correct one for computing the replacement fraction of Jaccard dissimilarity. PS and CCG correctly point out that the number of species replaced between two sites is $2\min(b,c)$ and this quantity expresses the number of species that would be unique to either sites if both sites were equally rich. However, to compute the

proportion of species that would be replaced if both sites were equally rich, one has to take into account that, in that case, the total number of species would no longer be $a + b + c$ (Fig. 1). In other words, the maximum number of species that can be replaced between two sites of different richness is not the total number of species ($a + b + c$), because the number of species in the poorest site establishes the limit of the total number of species that could be replaced at all.

This limit is $a + 2\min(b,c)$ and, therefore, this is the correct denominator corresponding to $2\min(b,c)$ and for building a dissimilarity measure that accounts for the turnover component of the Jaccard dissimilarity, which I introduce here:

$$\beta_{jtu} = \frac{2\min(b,c)}{a + 2\min(b,c)}. \tag{5}$$

Since in the absence of nestedness β_{jac} is equal to β_{jtu}, their subtraction ($\beta_{jne} = \beta_{jac} - \beta_{jtu}$) accounts for the fraction of Jaccard dissimilarity derived from richness differences between nested sites or, in other words, provides a measure of the nestedness component of the Jaccard dissimilarity:

$$\beta_{jne} = \frac{b+c}{a+b+c} - \frac{2\min(b,c)}{a+2\min(b,c)}$$
$$= \frac{\max(b,c) - \min(b,c)}{a+b+c} \times \frac{a}{a+2\min(b,c)}. \tag{6}$$

Table 1 provides a new unified terminology for these measures and those proposed in my previous paper (Baselga, 2010). Following the same procedure already used to build the multiple-site extensions for the Sørensen family (Baselga *et al.*, 2007; Baselga, 2010), multiple-site measures for the Jaccard family can be easily derived (Table 2).

The failure to adjust the correct numerator with the corresponding correct denominator makes the partition proposed by PS and CCG meaningless. If two sites have no species in common (as sites A–F in CCG, Fig. 1), irrespective of the existence of richness differences or not, this means that all species that could potentially be replaced have actually been replaced. Any meaningful measure of replacement (i.e. spatial turnover) should reflect this. Therefore, it makes no sense that, for sites A–F in CCG Fig. 1, the PS and CCG partitioning framework attributes a large fraction of the total dissimilarity ($\beta_{jac} = 1$) to the richness difference ($\beta_{rich} = 0.8$) and only a small fraction to species replacement ($\beta_{-3} = 0.2$). From another point of view, the problem can also be stated as follows: a measure of species replacement between two sites (i.e. spatial turnover) must be independent of richness differences, so adding unique species to only one of the sites should not affect the replacement measure. In contrast, any change in the proportion of species shared between two sites should be reflected by a meaningful measure of species replacement. None of these requirements are fulfilled by β_{-3} ($= R_{rel}$) (Figs 2 & 3).

WHAT THE TERNARY PLOTS TELL US

CCG provided a set of ternary plots showing the variation of the aforementioned dissimilarity measures for all possible propor-

Table 1 Overview of the pairwise dissimilarity measures mentioned in this paper, including names, proposed notation, formulae and references. Note that the nestedness-resultant component of Sørensen dissimilarity, previously denoted as β_{nes} (Baselga, 2010), is here re-notated as β_{sne} in order to allow it to be distinguished from the new nestedness-resultant component of Jaccard dissimilarity, β_{jne}.

Family	Measure	Notation	Formula	References
Sørensen (indices are relativized by $S_1 + S_2 = 2a + b + c$)	Sørensen dissimilarity	β_{sor}	$\dfrac{b+c}{2a+b+c}$	Sørensen (1948), Koleff *et al.* (2003)
	Simpson dissimilarity (= turnover component of Sørensen dissimilarity)	β_{sim}	$\dfrac{\min(b,c)}{a+\min(b,c)}$	Simpson (1943), Lennon *et al.* (2001), Koleff *et al.* (2003)
	Nestedness-resultant component of Sørensen dissimilarity	β_{sne}	$\dfrac{\max(b,c)-\min(b,c)}{2a+b+c}\times\dfrac{a}{a+\min(b,c)}$	Baselga (2010)
Jaccard (indices are relativized by $n = a + b + c$)	Jaccard dissimilarity	β_{jac}	$\dfrac{b+c}{a+b+c}$	Jaccard (1912), Koleff *et al.* (2003)
	Turnover component of Jaccard dissimilarity	β_{jtu}	$\dfrac{2\min(b,c)}{a+2\min(b,c)}$	This paper
	Nestedness-resultant component of Jaccard dissimilarity	β_{jne}	$\dfrac{\max(b,c)-\min(b,c)}{a+b+c}\times\dfrac{a}{a+2\min(b,c)}$	This paper

tions of the *a*, *b* and *c* components (i.e. the number of species present in both sites, the number of species unique to the first site and the number of species unique to the second site, respectively). These plots (Fig. 4 in CCG) are appealing, as they provide the whole spectrum of the respective indices for all combinations of *a*, *b* and *c*. However, the usefulness of ternary plots is undermined by the lack of specific examples, because the original *a*, *b* and *c* components are transformed to proportions (i.e. *a′*, *b′* and *c′*; see Koleff *et al.*, 2003), which are interdependent (i.e. they have to sum up to 1). For this reason, it is not intuitively obvious how the addition of unique species to a single site (i.e. incrementing richness differences) may change the position of a given pair of sites in the ternary plot or what the different structures in the ternary plots mean (i.e. the equilateral triangles in β_{-3} versus the obtuse isosceles triangles in β_{sim}).

The addition of unique species to one of the sites (Fig. 2) increases the *c* component but preserves unchanged the *a* and *b* components. When the components are transformed to proportions, it produces an increment of *c′*, and consequently a decline of *a′* and *b′*. In the case examples in Fig. 2, this means that cases A–F form a straight line from the centre of the ternary plot to the lower-right corner. Such a line passes across different values of β_{-3} (equilateral triangles in CCG's Fig. 4). As a result, β_{-3} decreases from cases A to F, whereas β_{sim} remains unchanged. If, as defined by CCG 'replacement between two sites is the substitution of *n* species in a given site from *n* species in another site', it makes little sense that β_{-3} finds that replacement is higher in A than in F. The number of species that are actually replaced [i.e.

2 min(*b,c*)] and the maximum number of species that could potentially be replaced [*a* + 2 min(*b,c*)] remain unchanged, because this maximum is determined by the poorest site. Thus, any meaningful measure of replacement must remain unchanged between cases A and F, as β_{sim} and β_{jtu} do (Fig. 2).

A second example implies the addition of species to the poorest site, these species being the same as already present in the richest site. This makes *a* and *a′* increase, while the number of unique species in the poorest site (*b* and *b′*) is kept constant, and the number of unique species at the richest site (*c* and *c′*) is reduced (Fig. 3). Under these conditions, cases G–L form a straight line parallel to the right side of the ternary plot. As can be seen in CCG's Fig. 4, such a line is contained in one of the constant bands for β_{-3}, whereas it crosses several regions for β_{sim}. Therefore, β_{-3} remains constant whereas β_{sim} declines from case G to case L. It is intuitive that if the number of replaced species remains constant but the number of shared species increases, any meaningful measure of replacement should decrease under these conditions. The reason again is that the ratio between the number of replaced species [2 min(*b,c*)] and the total number of species that could potentially be replaced [*a* + 2 min(*b,c*)] declines from G to L. Again β_{sim} and β_{jtu} do reflect this pattern, whereas β_{-3} does not.

THE BEHAVIOUR OF THE JACCARD AND SØRENSEN FAMILIES

At this point, one may wonder why the Jaccard and Sørensen families of indices differ in their denominator. In the case of the

Table 2 Overview of the multiple-site dissimilarity measures mentioned in this paper, including names, proposed notation, formulae and references. Note that the nestedness-resultant component of Sørensen dissimilarity, previously denoted as β_{NES} (Baselga, 2010), is here re-notated as β_{SNE} in order to allow distinguishing it from the new nestedness-resultant component of Jaccard dissimilarity, β_{JNE}.

Family	Measure	Notation	Formula	References
Sørensen	Sørensen dissimilarity	β_{SOR}	$$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}$$	Baselga (2010)
	Simpson dissimilarity (= turnover component of Sørensen dissimilarity)	β_{SIM}	$$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$$	Baselga *et al.* (2007), Baselga (2010)
	Nestedness-resultant component of Sørensen dissimilarity	β_{SNE}	$$\dfrac{\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]-\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{2\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}\times\dfrac{\sum_i S_i - S_T}{\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$$	Baselga (2010)
Jaccard	Jaccard dissimilarity	β_{JAC}	$$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}$$	This paper
	Turnover component of Jaccard dissimilarity	β_{JTU}	$$\dfrac{2\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right]+2\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$$	This paper
	Nestedness-resultant component of Jaccard dissimilarity	β_{JNE}	$$\dfrac{\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]-\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_i S_i - S_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}\times\dfrac{\sum_i S_i - S_T}{\left[\sum_i S_i - S_T\right]+2\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$$	This paper

Sørensen index ($\beta_{sor} = b + c/2a + b + c$), it should be noted that the denominator is $2a + b + c$ because here the total number of unique species ($b + c$) is relativized with respect to the sum of local richness in both sites (i.e. $S_1 + S_2 = 2a + b + c$). The rationale behind using this denominator is that β_{sor} yields the proportion of unique species per site, which is a measure of dissimilarity at least as meaningful as the proportion of unique species in the entire pool (β_{jac}). Thus, when the correct numerator accounting for species replacement is relativized with respect to what would be the sum of S_1 and S_2, if both sites were equally rich, one arrives at the Simpson index [$2 \min(b,c)/2a + 2 \min(b,c) = \min(b,c)/a + \min(b,c)$]. Thus, despite CCG's claim, the replacement in β_{sim} is indeed mathematically equivalent to the replacement in β_{sor}. Their difference ($\beta_{sne} = \beta_{sor} - \beta_{sim}$) accounts for the nestedness-resultant fraction of β_{sor} (Baselga, 2010). Note that the nestedness-resultant component of Sørensen dissimilarity, previously denoted as β_{nes} (Baselga, 2010), is here re-notated as

β_{sne} in order to allow distinguishing it from the new nestedness-resultant component of Jaccard dissimilarity, β_{jne}.

The monotonic relationship between β_{sor} and β_{jac} is well known, as both are monotonic transformations of multiplicative beta diversity (Jost, 2007). This relationship is described by the equation $\beta_{sor} = 2\beta_{jac}/(1 + \beta_{jac})$ (see, for example, Soininen *et al.*, 2007). However, the relationship is not linear (Fig. 4a). β_{sor} gives more weight to the shared species a because of the aforementioned different rationales introduced by the different denominators (unique species by site in β_{sor}, versus unique species by entire pool in β_{jac}). A similar monotonic relationship holds for the turnover components of β_{sim} and β_{jtu} (Fig. 4b) but not for the nestedness components of β_{sne} and β_{jne} (Spearman rank correlation $\rho = 0.980$; Fig. 4c). Deviations from the monotonic relationship are related to (1) the existence richness differences (i.e. non-zero nestedness-component) and (2) the nonlinear relationship between the turnover components
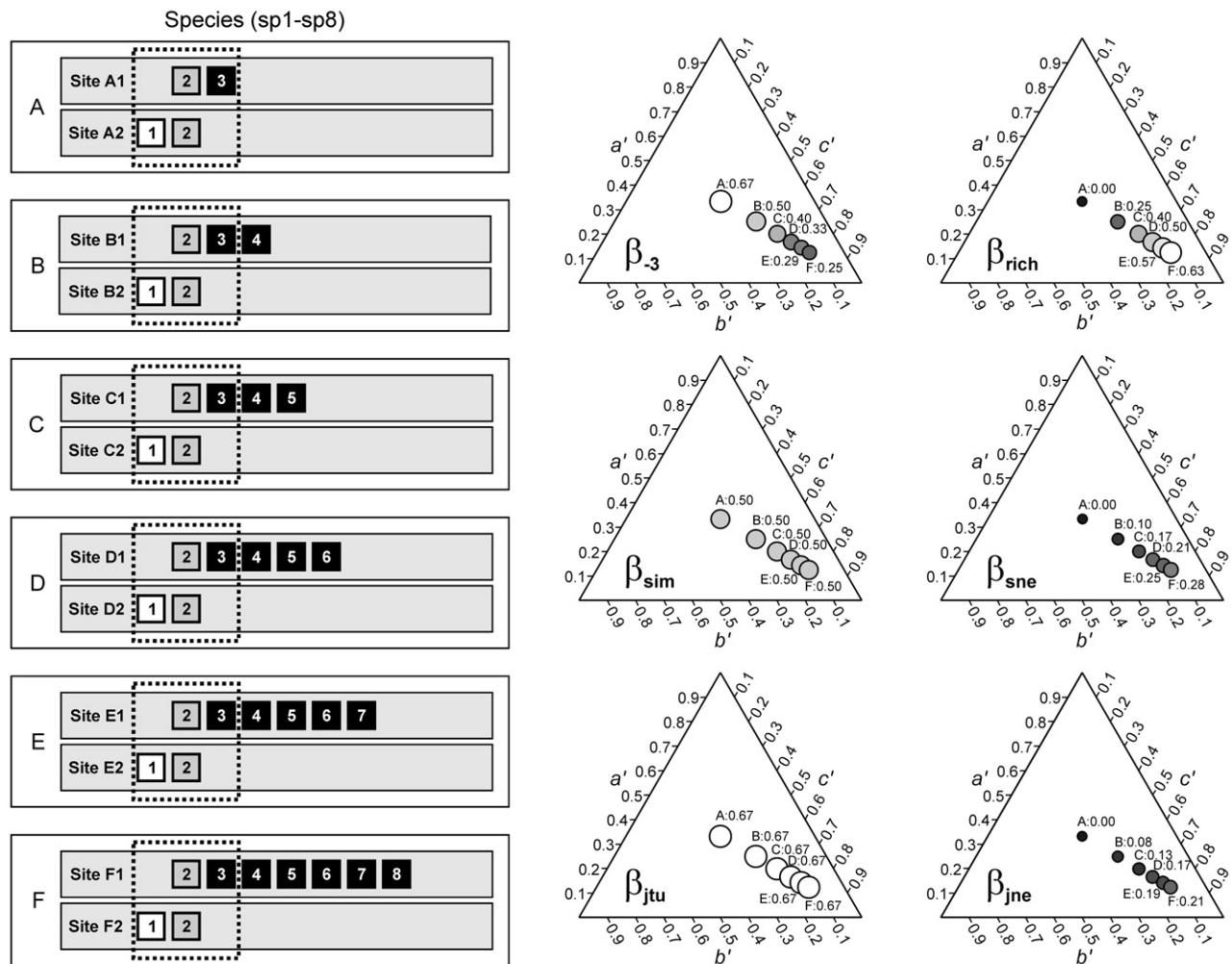
Figure 2 Hypothetical examples illustrating the performance of measures. The ternary plots show the values of different dissimilarity measures for the cases A–F. Dissimilarity values are represented by grey tones and the size of dots. The addition of unique species to the richest site implies a reduction of β_{-3}, whereas β_{sim} and β_{jtu} remain unchanged. Dotted squares indicate what would be the species composition if both sites were equally rich. See main text for further discussion.

caused by the different denominator (i.e. β_{sim} measures the proportion of unique species per site if both sites where equally rich, while β_{jtu} measures the proportion of unique species in the two sites pooled together if both sites were equally rich). Thus, the largest deviations from the linear relationship occur when richness differences are large (i.e. $b \gg c$ or $b \ll c$) and either of these conditions is met: (1) $\max(b,c) = a$ or (2) $\min(b,c) = a$. In the first case, when $\max(b,c) = a$ the difference between β_{sor} and β_{jac} is at its maximum because they use a different logic for relativizing the number of unique species (0.33 and 0.50 in the example in Fig. 4a, in which $a = 1000$, $b = 1000$, $c = 1$), while there is obviously almost no species replacement so both β_{sim} and β_{jtu} yield values very close to zero. In the second case, when $\min(b,c) = a$ both β_{sor} and β_{jac} detect that the dissimilarity is almost complete (0.98 and 0.99 in the example in Fig. 4a, in which $a = 1$, $b = 1000$, $c = 1$), while the difference between β_{sim} and β_{jtu} is maximum because of their different logics for relativizing the number of unique species (Fig. 4b). However, only the

last situation produces deviations from the 1:1 relationship between the proportions of overall dissimilarity (β_{sor} or β_{jac}) that are attributed to any of the components (spatial turnover or nestedness-resultant dissimilarity). Consequently, the relationship between the ratios between components and total dissimilarity is not monotonic (i.e. Fig. 4d & e) but the Spearman rank correlation is high ($\rho = 0.998$). Therefore, the use of the Jaccard and Sørensen families of indices is roughly equivalent.

REPLACEMENT AND NESTEDNESS

PS aimed for a unified framework for combining nestedness, beta diversity and their respective fractions that can be plotted together using a two-dimensional simplex. Thus, even if R_{rel} has been proved here to be an inconsistent measure of species replacement, N_{rel} could still be a measure of nestedness or dissimilarity due to nested patterns. However, it is evident that R_{rel} and N_{rel} are not measuring different phenomena, because $N_{rel} =$
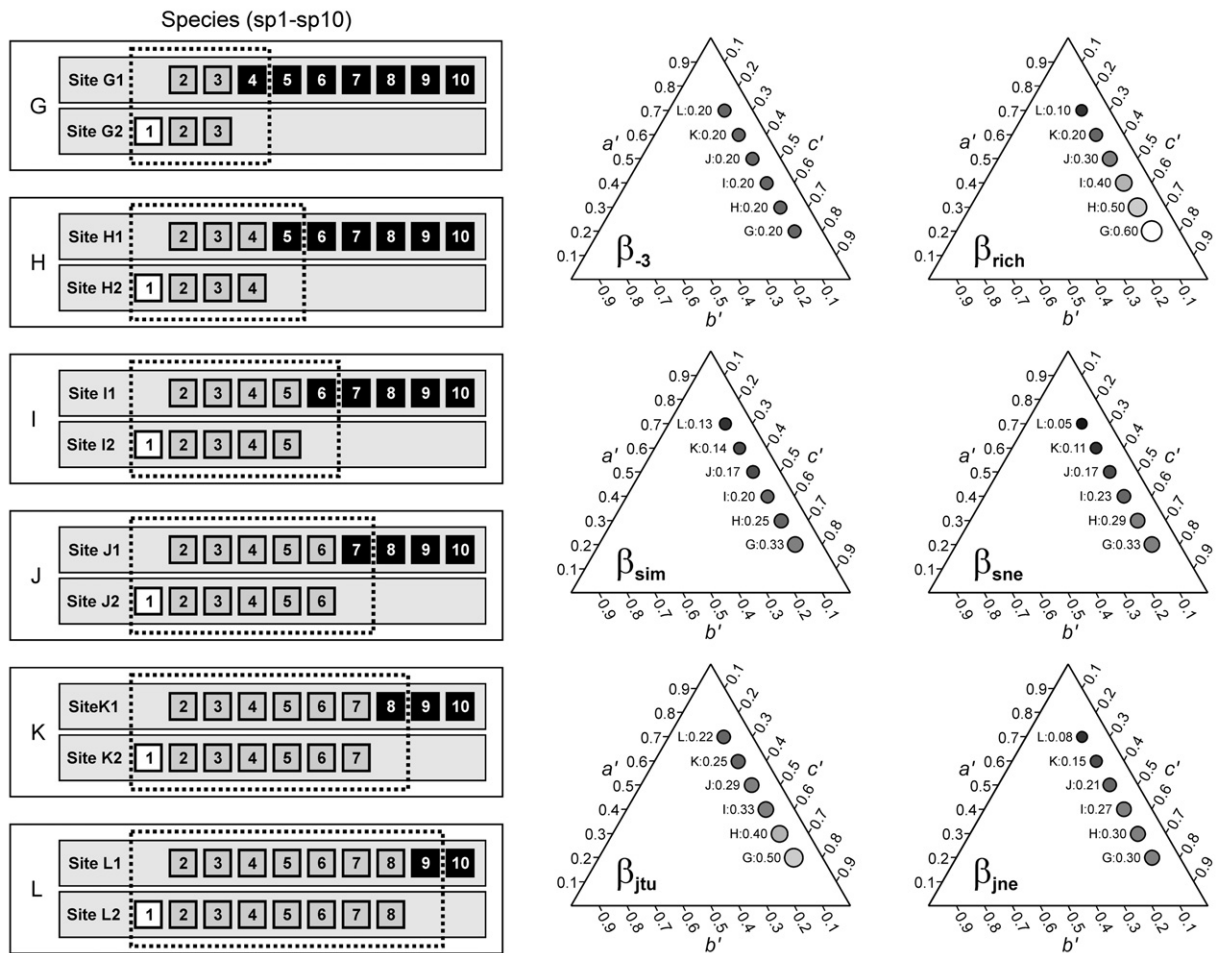
Figure 3 Hypothetical examples illustrating the performance of measures. The ternary plots show the values of different dissimilarity measures for the cases A–F. Dissimilarity values are represented by grey tones and the size of dots. The addition of species to the poorest site increasing the number of shared species implies no variation in β_{-3}, whereas β_{sim} and β_{jtu} decline in parallel with the reduction of the ratio between the number of species replaced and the number of species that could potentially be replaced. Dotted squares indicate what would be the species composition if both sites were equally rich. See main text for further discussion.

$1 - R_{rel}$ (i.e. one quantity completely determines the other). Thus, they are in fact the same measure, in the very same sense that Jaccard similarity (a/n) and Jaccard dissimilarity ($b + c/n$) are the same measure, because Jaccard dissimilarity = $1 -$ Jaccard similarity. The consequence of accepting these definitions of replacement and nestedness, derived from the measures proposed by PS is that we would no longer need two different concepts (nestedness and species replacement) as they would be the same thing. In other words, if we measured the dissimilarity between two sites due to species replacement, we would also know the degree of nestedness automatically. Moreover, the same simple examples (Fig. 2 cases G–L) show that N_{rel} neither measures nestedness itself nor the dissimilarity caused by nestedness. The difference between b and c decreases from case G to case L, while a increases simultaneously, so that the dissimilarity due to the nested patterns decreases from G to L. However, N_{rel} remains unchanged. As for nestedness itself, although there are different definitions (Wright & Reeves, 1992; Almeida-Neto *et al.*, 2008; Ulrich *et al.*, 2009), a measure

that considers equally nested cases G to L (as it does for 'perfect nestedness', 'maximum fill' and 'minimum fill' examples in PS's Fig. 3) seems of little use, as it does not take into account matrix filling, which, according to Almeida-Neto *et al.* (2008), is one of the basic features determining the degree of nestedness. I agree with Almeida-Neto *et al.* (2008) that a useful concept of nestedness depends both on paired overlap and matrix filling, such that nestedness (1) is maximum when all of the poorest sites are subsets of the richest sites and filling is intermediate, and (2) declines to both extremes of the matrix filling or when species replacement disrupts the nested pattern. For this reason the model 'perfect nestedness' in PS's Fig. 3 has been so named. Accepting this definition of nestedness allows one to measure replacement and nestedness as two different patterns, which are indeed related (i.e. no replacement can occur when nestedness is perfect, and no nestedness occur when replacement is perfect) but not the same thing (i.e. at intermediate values of nestedness different degrees of species replacement are possible, and vice versa).
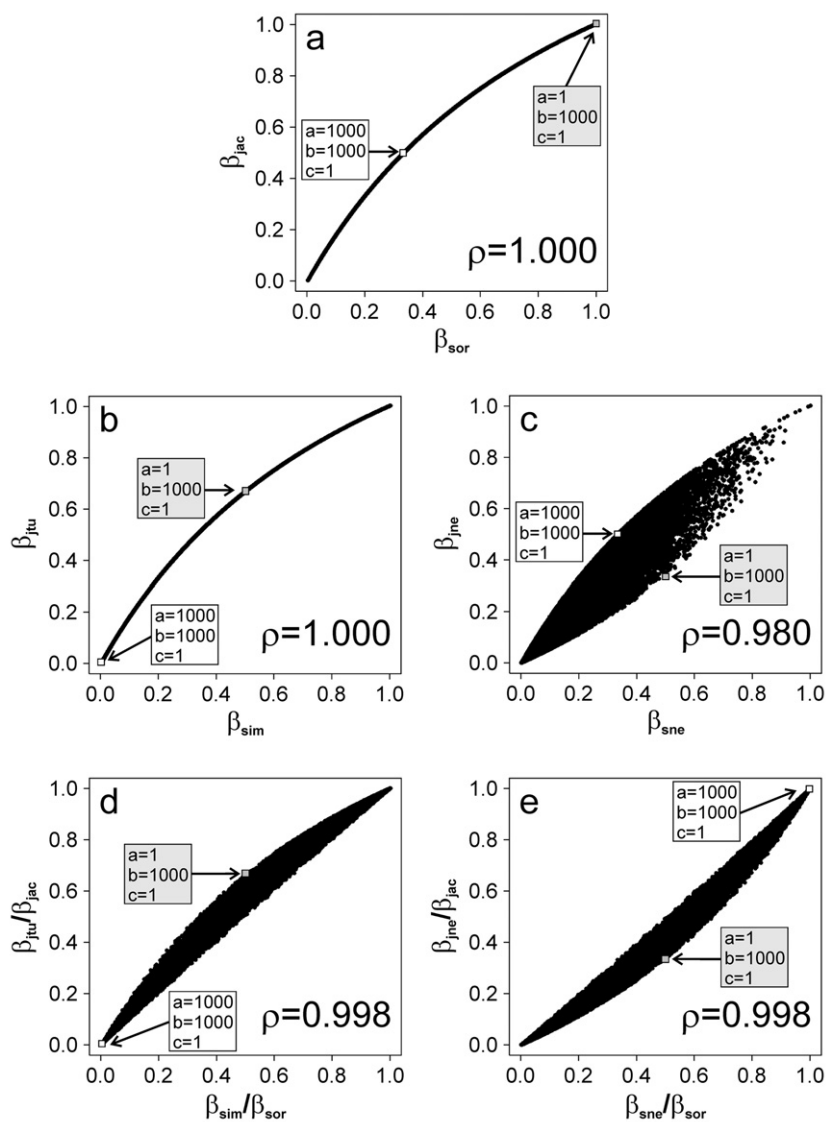
Figure 4 Relative behaviour of the Sørensen and Jaccard families of indices: (a) relationship between Sørensen and Jaccard indices; (b) relationship between the turnover components, β_{sim} and β_{jtu}; (c) relationship between the nestedness components β_{sne} and β_{jne}; (d) relationship between the ratios β_{jtu}/β_{jac} and β_{sim}/β_{sor}; (e) relationship between the ratios β_{jne}/β_{jac} and β_{sne}/β_{sor}. Relationships were explored using simulations performed in R, taking 100,000 random combinations of a, b and c matching components from uniform distributions between 1 and 1000. Grey and white squares represent particular situations (whose matching components a, b, and c are shown), used to exemplify deviations from monotonic relationships. Spearman rank correlations (ρ) are shown. See main text for further explanation.

NESTEDNESS AND THE NESTEDNESS COMPONENT OF BETA DIVERSITY

The relationship between the nestedness component of Sørensen dissimilarity (β_{sne}) and nestedness (as measured by NODF – Nestedness metric based on Overlap and Decreasing Fill) has been recently explored by AFU. To do this the cited authors tested three expectations that were derived by deduction. According to these predictions, β_{sne} and β_{SNE} should (1) increase with nestedness, (2) should not vary with constant nestedness, and (3) should be zero in the absence of nestedness. In my opinion only the third expectation is justified.

As for the first expectation, I have shown in my original contribution (Baselga, 2010: Fig. 4) that in a set of nested matrices the nestedness component of beta diversity increases with decreasing matrix filling, while nestedness is maximum at intermediate filling. AFU replicate this example, and conclude that β_{sne} and β_{SNE} do not measure the nestedness component of

beta diversity because they are not monotonically related to NODF. However, AFU themselves call the five matrices involved in their example (AFU's Fig. 1a–g) 'nested matrices'. This is because the only differences in composition that exist in any of these matrices are nested patterns. In other words, the only pattern behind dissimilarity in these matrices is nestedness, and dissimilarity increases from matrix (a) to matrix (g), as measured by β_{SNE}. Note that any traditional measure of beta diversity as Whittaker's β (i.e. gamma/mean alpha) or its ranged version β_{-1} have the same behaviour (i.e. increase from a to g), so β_{SNE} is correctly capturing the increment in total dissimilarity. Also, it is correctly capturing that the total dissimilarity is derived only from a nested pattern, because β_{SNE} is equal to β_{SOR} in all the matrices. In other words, what β_{SNE} does not measure is how perfect the nested pattern is, as NODF would measure, but it does measure how dissimilar the sites are due to a nested pattern or, in short, due to nestedness. Another enlightening conclusion that can be extracted from

this example is the basic incorrectness of using the mean pairwise measures for computing multiple-site dissimilarities. As shown in AFU's Fig. 2(b), the mean pairwise β_{sne} does not monotonically increase from matrix (a) to matrix (g). Again, in all of these matrices β_{sne} is equal to β_{sor}, which means that the mean of Sørensen dissimilarities is not monotonically related to Whittaker's β or β_{-1}, which indeed monotonically increase from matrix (a) to (g). Therefore, as shown by previous authors (Diserud & Ødegaard, 2007), I stress again the need to use multiple-site dissimilarity measures when the attribute of interest involves more than two sites, as the use of averaged pairwise measures can yield misleading results.

Regarding the second expectation (i.e. β_{SNE} should not vary with constant nestedness), the previous example has already shown that this expectation is not justified when the concept of dissimilarity due to nestedness (or the nestedness component of dissimilarity) is clearly differentiated from nestedness itself. For example, matrices (a) and (g) have the same nestedness (as measured by NODF), but a different dissimilarity due to nestedness. This is by no means undesirable, but instead reflects that the dissimilarity caused by nested patterns increases with decreasing matrix filling. The next example shown by AFU in their Fig. 3 is of little use because it compares matrices with different number of sites and β_{SNE} is affected by the number of sites involved in the calculation (Baselga, 2010). The inability to compare matrices with different number of sites is indeed an undesirable property of β_{SOR}, β_{SIM} and β_{SNE} (Baselga, 2010) and further research should be devoted to investigate whether a better solution for building these indices can be found. However, this behaviour does not imply that β_{SNE} yields comparatively larger fractions of dissimilarity derived from nestedness when matrix size increases, because the same relationship between dissimilarity and matrix size occurs for β_{SOR} and β_{SIM}. In the case of pairwise indices, I should stress again the basic incorrectness of using averaged pairwise measures for characterizing multiple-site beta-diversity values (see above). In sum, what AFU's result shows is that the multiple-site dissimilarity as developed in my previous contribution (Baselga, 2010) can only be compared when the number of sites is kept constant (as already shown in Baselga, 2010; Fig. 3).

Finally, the third expectation tested by AFU (i.e. β_{sne} and β_{SNE} should be zero in the absence of nestedness) is indeed a justified one. If we analyse the formula of the pairwise index,

$$\beta_{sne} = \frac{\max(b,c) - \min(b,c)}{2a + b + c} \times \frac{a}{a + \min(b,c)}, \qquad (7)$$

it can easily be seen that β_{sne} can only take non-zero values in the presences of nestedness. This is because the second term of the formula [i.e. $a/a + \min(b,c)$] is a measure of nestedness for pairwise situations (AFU's equation 5). Therefore, in the absence of nestedness β_{sne} is always zero, and in the presence of nestedness β_{sne} takes a value determined by the richness differences (first term of the equation), conditioned by the degree of nestedness between sites. In the case of the multiple site extension, β_{SNE}, AFU convincingly show that the index can take non-

zero values in the absence of nestedness. I agree with AFU that this is a completely undesirable property. The underlying reason is again the way in which the matching component analogues were built. The multiple-site analogue for the matching component a, $\sum S_i - S_T$, is not zero even if the poorest localities are not nested in the richest ones. However, AFU's analysis of the Atmar and Patternson empirical dataset shows that these situations are probably extremely rare in the real world (AFU's Fig. 4b). In fact, no matrix with a low nestedness value yielded a large value of β_{SNE}.

CONCLUSIONS

The partitioning approaches proposed by PS and CCG are identical and cannot be recommended because the partitioned components of beta diversity do not reflect meaningful ecological concepts. More specifically, the numerator in β_{-3} ($= R_{rel}$) accounts for the number of species that are replaced, whereas the denominator accounts for the total number of species and not the total number of species that could potentially be replaced. For this reason, β_{-3} ($= R_{rel}$) underestimates species replacement when richness differences exist. Consequently, since the CCG and PS partitions are additive, β_{rich} ($= D_{rel}$) overestimates the fraction of total dissimilarity that can be attributable to richness differences. Furthermore, the PS framework is not useful for assessing nestedness, as it equates nestedness with β_{-3}, a measure that does not account for matrix filling. Instead, nestedness patterns should be assessed using consistent measures that depend both on paired overlap and matrix filling, as for example NODF (Almeida-Neto et al., 2008), and beta-diversity patterns should be assessed using measures that allow the separation of the fractions of dissimilarity derived from species replacement or from nestedness (Baselga, 2010). In the case of multiple-site dissimilarity patterns, averaged pairwise indices should never be used because the mean of pairwise values is unable to accurately reflect the multiple-site attributes of dissimilarity. Multiple-site dissimilarity measures are thus mandatory when the attribute of interest is the variation in species composition among more than two sites. Unfortunately, the multiple-site measures developed here and in my previous contributions (Baselga et al., 2007; Baselga, 2010) present some undesirable properties, e.g. they can yield non-zero values in the absence of nestedness in some special situations. Therefore, future research should be devoted to building better multiple-site extensions of dissimilarity indices. However, empirical results show that the potential biases are generally not present in real data, and thus that the current multiple-site indices should be considered the best available approximation for separating the contribution of turnover and nestedness to multiple-site dissimilarity.

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BIOSKETCH

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