Measuring fractions of beta diversity and their relationships to nestedness: a theoretical and empirical comparison of novel approaches

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Beta diversity and nestedness are central concepts of ecology and biogeography and evaluation of their relationships is in the focus of contemporary ecological and conservation research. Beta diversity patterns are originated from two distinct processes: the replacement (or turnover) of species and the loss (or gain) of species leading to richness differences. Nested distributional patterns are generally thought to have a component deriving from beta diversity which is independent of replacement processes. Quantification of these phenomena is often made by calculating a measure of beta diversity, and the resulting value being subsequently partitioned into a contribution by species replacement plus a fraction shared by beta diversity and nestedness. Three methods have been recently proposed for such partitioning, all of them based on pairwise comparisons of sites. In this paper, the performance of these methods was evaluated on theoretical grounds and tested by a simulation study in which different gradients of dissimilarity, with known degrees of species replacement and species loss, were created. Performance was also tested using empirical data addressing land-use induced changes in endemic arthropod communities of the Terceira Island in the Azores. We found that the partitioning of β_{cc} (dissimilarity in terms of the Jaccard index) into two additive fractions, β_{-3} (dissimilarity due to species replacement) plus β_{rich} (dissimilarity due to richness differences) reflects the species replacement and species loss processes across the simulated gradients in an ecologically and mathematically meaningful way, whilst the other two methods lack mathematical consistency and prove conceptually self-contradictory. Moreover, the first method identified a selective local extinction process for endemic arthropods, triggered by land-use changes, while the latter two methods overweighted the replacement component and led to false conclusions. Their basic flaw derives from the fact that the proposed replacement and nestedness components (deemed to account for species loss) are not scaled in the same way as the measure that accounts for the total dissimilarity (Sørensen and Jaccard indices). We therefore recommend the use of $\beta_{cc} = \beta_{-3} + \beta_{rich}$, since its components are scaled in the same units and their responses are proportional to the replacement and the gain/loss of species.

Beta diversity has been interpreted mostly as the extent of change in community composition (Whittaker 1960, Koleff et al. 2003) along a given gradient and may also be understood as variation among sampling units without any specific reference to gradients (Anderson et al. 2011). In any case, beta diversity patterns are originated from two distinct processes, the replacement and the loss (or gain) of species. Of the two, only the loss (or gain) of species causes richness differences from site to site. When losses or gains occur in a more or less ordered manner, community pattern becomes nested (Atmar and Patterson 1993). In general, nestedness refers to the extent to which species of a smaller assemblage are a subset of a larger assemblage and is therefore a particular case of richness differences

(Almeida-Neto et al. 2008, Ulrich et al. 2009). In nature, the replacement and loss (or gain) of species are combined in an infinite number of ways, leading to complex patterns of community dissimilarity. Therefore, to understand the origins of beta diversity, nestedness and their causes, one has to determine the relative roles of replacement and richness differences.

The necessity of decomposing measures of beta diversity and nestedness into comparable fractions is thus obvious. Indeed, the idea of partitioning beta diversity into different components is not new. Several authors have used various measures with different properties in order to differentiate the influence of replacement and species loss on the origins of beta diversity (Harrison et al. 1992,

Williams 1996, Lennon et al. 2001, Melo et al. 2009). Nevertheless, none of these contributions established a comprehensive and unified framework for partitioning beta diversity. Recently, several attempts have been made to bridge this gap. The first one is due to Baselga (2010) proposed a general framework for unifying the different components of beta, suggesting partitioning pairwise beta diversity expressed by the Sørensen dissimilarity into replacement (turnover) and 'nestedness resultant' components. An alternative solution has also been proposed independently by Podani and Schmera (2011) and Carvalho et al. (2012). In this, beta diversity is measured by Jaccard dissimilarity which is decomposed into replacement and richness difference fractions. The richness difference fraction is taken as a positive contributor to a nestedness measure suggested by Podani and Schmera (2011). Even more recently, Baselga (2012) has rejected this suggestion and proposed decomposing Jaccard dissimilarity in the same fashion as the Sørensen index. Unfortunately, these different methods can lead to radically different conclusions about the same dataset (Carvalho et al. 2012) making inevitable the comparison of these approaches so that users of either approach can learn their relative merits and potential pitfalls and limitations.

In this paper, we argue that any partitioning of beta diversity should reflect properly the replacement and the loss (or gain) of species in order to be useful and ecologically meaningful. We review the concepts behind the different frameworks and the consistency of their performance with this expectation. For simplicity, we will focus only on pairwise comparisons of assemblages, although the conclusions could be extended to multiple-assemblage comparisons. First, we shall use arithmetic equations and small artificial examples to provide well defendable mathematical support for our arguments and to allow the reader to interpret the performance of the competing numerical approaches in a clear way. Then, our arguments are supported further by simulated examples and an actual case study on changes of the endemic arthropod fauna of Terceira Island (Azores, Portugal).

Existing methods for partitioning beta diversity

To save space, an overview of abbreviations and the mathematical formalism is summarized in tabular form (Table 1). Note that replacement and (species) turnover are regarded as synonyms. The method proposed by Baselga (2010) consists in partitioning pairwise Sørensen dissimilarity (β_{sor}) into two components: dissimilarity due to species replacement (β_{sim}) plus dissimilarity due to nestedness (β_{nes})

$$\beta_{sor} = \beta_{sim} + \beta_{nes}$$

The rationale of this method is based on the fact that β_{sor} is sensitive to replacement and richness differences and β_{sim} (well-known as Simpson dissimilarity) seems to be sensitive to replacement only. Because, in the absence of nestedness, $\beta_{sor} = \beta_{sim}$, Baselga deduced that $\beta_{sor} - \beta_{sim}$ would yield a measure of dissimilarity due to nestedness (β_{nes}).

Table 1. Measures used in the different partitioning frameworks in which a is the number of shared species between two sites, b and c are the numbers of exclusive species of either site (Koleff et al. 2003).

Metric	Notation	Reference
β_{sor}	$\dfrac{b+c}{2a+b+c}$	Sørensen 1948
β_{sim}	$\dfrac{\min(b,c)}{a+\min(b,c)}$	Simpson 1943 Lennon et al. 2001
β_{nes}	$\dfrac{|b-c|}{2a+b+c} \times \dfrac{a}{a+\min(b,c)}$	Baselga 2010
β_{cc} (or β_{jac})	$\dfrac{b+c}{a+b+c}$	Jaccard 1912 Colwell and Coddington 1994
β_{-3}	$2 \times \dfrac{\min(b,c)}{a+b+c}$	Williams 1996 Cardoso et al. 2009a
β_{rich}	$\dfrac{|b-c|}{a+b+c}$	Schmera and Podani 2011 Carvalho et al. 2012
β_{jtu}	$2 \times \dfrac{\min(b,c)}{a+2\min(b,c)}$	Baselga 2012
β_{jne}	$\dfrac{|b-c|}{a+b+c} \times \dfrac{a}{a+2\min(b,c)}$	Baselga 2012

The performance of Baselga's (2010) method was found to be inconsistent with the variation of species replacement and species loss (Podani and Schmera 2011, Schmera and Podani 2011, Almeida-Neto et al. 2012, Carvalho et al. 2012). A new partitioning of beta diversity, due to Podani and Schmera (2011) and Carvalho et al. (2012) provides formal definitions of both absolute and relativized measures in terms of the parameters of the 2×2 contingency table (Table 1). Absolute beta diversity is expressed as $b + c$ (Weiher–Boylen beta, Koleff et al. 2003), which is divided into species replacement and richness difference fractions. The term replacement means that a species in one site is substituted by a species in another site (or point of time in the same site). Therefore, one replacement always involves two species and the total number of replaced species is equal to $2\min(b, c)$. Richness differences arise from the loss (or gain) of species and are measured as $|b - c|$. Therefore, the contingency table can be algebraically decomposed into two biologically sound asymmetric components, according to the expression:

$$b + c = 2\min(b, c) + |b - c|$$

(Fig. 1). Under this framework, nestedness is conceived, in absolute terms, as the sum of two independent components, overlap (a) and richness difference ($|b - c|$) with the condition $a > 0$ (Podani and Schmera 2011, 2012).

Relativization of beta diversity may be achieved by division with the total number of species of the system ($n = a + b + c$), which has an obvious theoretical link to the gamma diversity concept as applied to pairs of sites. Thus, we have the Jaccard dissimilarity β_{cc} (β_{jac} in Baselga' notation) which can be decomposed into relativized species replacement or dissimilarity due to replacement (β_{-3}, or R_{rel} in Podani and Schmera's notation) and
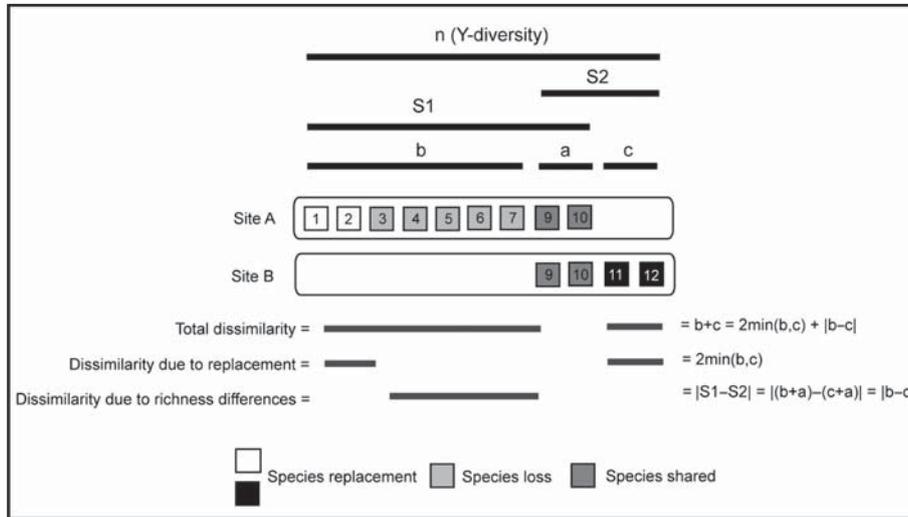
Figure 1. Algebraic decomposition of beta diversity (total dissimilarity = b + c) of a pairwise system into two additive components, species replacement (2min(b, c)) plus richness difference (|b − c|). These quantities can be scaled in two different ways: 1) in relation to the number of species in the system (*n*), which is theoretically linked to the notion of gamma (γ) diversity, 2) to the sum of species of both sites (S1 + S2). In the present example, richness differences, resulting from the loss of six species from site A to site B, contributed more to the total dissimilarity than replacement (four species). However, β_{sim} (0.50) > β_{nes} (0.21) and β_{jtu} (0.67) > β_{jne} (0.17), contrary to β_{-3} (0.33) < β_{rich} (0.5).

relativized richness difference or dissimilarity due to richness differences (β_{rich} or D_{rel}), as given below

$$\beta_{cc} = \beta_{-3} + \beta_{rich}$$

Relativized nestedness (N_{rel}) is understood as the sum of Jaccard similarity (overlap) and relativized richness difference, with the same condition as above. It is seen immediately that there is a fraction shared by beta diversity and nestedness, namely richness difference, either absolute or relativized (Podani and Schmera 2011, 2012, which may also be consulted for other pairwise measures of nestedness and their comparative evaluation). Although, the definition of nestedness differs with studies (Ulrich et al. 2009), our approach establishes a conceptual and methodological link between beta diversity and nestedness, and facilitate understanding and application of these measures in ecology and biogeography. (Note that we did not give any decomposition related to Sørensen dissimilarity because double weighted overlap scores in this coefficient do not apply to any meaningful definition of nestedness.)

However, Baselga (2012) has rejected the above suggestions. Following the same rationale he used for partitioning β_{sor} into replacement and nestedness-resultant dissimilarity, he proposed a similar partitioning of β_{cc} into dissimilarity due to replacement (β_{jtu}) plus dissimilarity due to nestedness (β_{jne}), such that:

$$\beta_{cc} = \beta_{jtu} + \beta_{jne}$$

Theoretical issues

Scaling

In comparing the alternative approaches, let us first examine the scaling of coefficients involved in the decomposition of beta diversity. In the partitioning of β_{sor}, Baselga (2010)

scaled total dissimilarity (b + c) to the sum of species richness scores of both sites (2a + b + c), whilst replacement (2min(b, c)) was scaled to what would be the species richness of each site if 'both sites were equally rich' (a + min(b, c)), resulting in the β_{sim} index. In the partitioning of β_{cc}, Baselga (2012) scaled total dissimilarity (b + c) to the total number of species of the pairwise system (a + b + c), whilst replacement (2min(b, c)) was scaled to the quantity a + 2*min(b, c) assumed to establish the 'limit of the total number of species that could be replaced at all'. It is seen immediately that the replacement fractions implicitly included in β_{sor} and β_{cc} are not mathematically and conceptually equivalent to the replacement given by β_{sim} and β_{jtu}, respectively.

The scaling problem has been illuminated numerically by small artificial examples in Schmera and Podani (2011). Nevertheless, in order to have a complete picture on the subject matter in this communication as well, we provide another convincing example. Suppose that a = 3, b = 5 and c = 2. From these values we obtain that β_{sor} = 7/13, β_{sim} = 2/5 and β_{nes} = 9/65 (since 7/13 − 2/5 = 3/13 × 3/5 = 9/65). While β_{sor} expresses the proportion of total presence scores (i.e. 2a + b + c = 13) that are not shared by the two sites, β_{sim} corresponds to the proportion of presence scores in the poorer site (a + min(b, c) = 5) which are not present in the other site. The value of 9/65, however, does not reflect any reasonable quantity in terms of species numbers and their proportions. The reason is that Sørensen dissimilarity and Simpson dissimilarity are differently scaled (to 13 versus 5), notwithstanding that they have the same range (0 to 1). Subtracting a quantity from another is indeed incorrect logically if the measurement units or the scale of the two are not identical. We may thus conclude that Simpson dissimilarity is an unjustified choice for measuring replacement, if beta diversity is expressed by Sørensen dissimilarity.

The decomposition of β_{cc} as suggested by Baselga (2012) suffers from the same drawback as that of β_{sor}: different scaling and therefore lack of common currency. Using the same example as above, $\beta_{jne} = \beta_{cc} - \beta_{jtu} = 7/10 - 4/7 = 9/70$. Similarly to the previous case, we are unable to attribute any meaning to this result, so that any suggestion as to the direct ecological interpretation of this value in terms of absolute species numbers or their proportions would be warmly welcome. β_{jtu} is apparently a less fortunate choice for quantifying species replacement if beta diversity is expressed by the Jaccard index.

By contrast, our approach offers easy interpretation of results both 'mathematically' and 'ecologically'. For the same example as above, the meaning of absolute values is straightforward: $b + c = 7$ is the number of species not shared by the two sites (beta), $2\min(b, c) = 4$ is species replacement and $|b - c| = 3$ is richness difference. By standardization with n ($= 10$), we obtain the Jaccard index, $\beta_{cc} = 7/10$, relativized species replacement, $\beta_{-3} = 4/10$, and relativized richness difference component, $\beta_{rich} = 7/10 - 4/10 = 3/10$. In words, 7/10 is the proportion of the total number of species in which the two sites differ, 4/10 is species turnover relative to the total number of species and 3/10 is the proportional difference in site counts. Thus, there is a common currency for all component terms, both absolute and relativized, therefore the algebraic relationship between total dissimilarity and species replacement is maintained (Fig. 1) and the ecological meaning of all these terms is straightforward.

On maximum replacement

As discussed above, scaling has to do with the maximum possible value of a coefficient. Therefore, it is highly relevant here to examine the rationale for choosing $a + 2\min(b, c)$ (Baselga 2012) as the maximum value of species replacement when beta diversity is measured by β_{cc}. This quantity is chosen on the grounds that 'the number of species in the poorest site establishes the limit of the total number of species that could be replaced at all' (Baselga 2012, p. 3, right column in the Early View document). A key element in this rationale is that this limit is the number of species 'that could potentially be replaced' if the two sites were equally rich, so that the turnover component becomes 'independent' of the richness difference between the localities. Without entering into details regarding what 'correctness' may mean in this case, we might accept at first glance that $2\min(b, c)/(a + 2\min(b, c))$ is meaningful under certain circumstances to measure replacement as a self-contained formula. However, there are several problems that prevent us to accept the proposition to take it either as a component of Jaccard dissimilarity or as a stand-alone coefficient. Our arguments can be summarized briefly as follows.

- The suggestion that the denominator in the replacement component of the Jaccard dissimilarity (β_{jtu}) should be $a + 2\min(b, c)$ and its explanation ('because the number of species in the poorest site establishes the limit of the total number of species that could be replaced at all') are contradictory because the number of species in the poorest site equals to $a + \min(b,c)$ and not to $a + 2\min(b, c)$.

- We do not see any reason why only the poorer site should establish the theoretical upper limit of species replacement. It is therefore useful to examine under which circumstances can $a + 2\min(b, c)$ be the maximum. Assume first that the total number of species in the two sites is constant, so the theoretical maximum can only be determined by breaking up joint presences in the data. The use of $a + 2\min(b, c)$ as denominator implies that maximum is reached when a/2 species remain only in site 1 and a/2 species in the other (Fig. 2A–B). Complications may arise, of course, when 'a' is an odd number. Nonetheless, the two sites can be 'potentially' equally rich and replacement even higher if the set of shared species is split between the sites such that their richness difference is compensated for (Fig. 2A, 2C). The extent to which this compensation is possible is determined by $|b - c|$, so that the maximum of species replacement can be higher than $a + 2\min(b, c)$ and is in fact constrained by both sites whenever $|b - c| > 0$. We can imagine another reasonable solution in which the number of species in each site remains constant and the total number of species increases. As seen in Fig. 2D, in this case the maximum is $2a + 2\min(b, c)$, larger than what Baselga (2012) proposed.

- However, when interest lies in the replacement component of Jaccard dissimilarity, then there is no reason to consider at all what the maximum of replacement can be; interest is merely focused on the absolute or relative contribution of the subset of species that are actually responsible for replacement. For this purpose, the use of 'n' (gamma diversity) as the denominator is the correct and, in fact, the only meaningful choice. We disagree with the proposal, therefore, that the rationale behind measures of species replacement 'dictates' (as stated in Baselga 2012) the choice of the denominator as the number of species that could potentially be replaced.

- The proposed replacement formula $2\min(b, c)/(a + 2\min(b, c))$ does not satisfy the requirements set up by Baselga (2012, p. 3, right column in the Early View document) himself, namely, that 'adding unique species to only one of the sites should not affect the replacement measure'. If a new species is added to the species poorer site, then the replacement measure suggested by Baselga (2012) does change. (For example, for $a = 5$, $b = 4$, and $c = 1$, we obtain 2/7, whereas for $a = 5$, $b = 4$ and $c = 2$, we get 4/9). Addition of this new species clearly modifies the nominator and the denominator, thus the 'proportion' of the species shared as well, so that the above requirement is in clear conflict with the following one 'any change in the proportion of species shared between two sites should be reflected by a meaningful measure of species replacement' (Baselga 2012, p. 3, right column in the Early View document). It was specified by Baselga (2012) as the second main property that a meaningful replacement function must have. Confusion around admissible properties of the replacement index probably came from the fact that in Fig. 1 of Baselga (2012) changes are monitored over increases of n, while n remains constant in his Fig. 2.
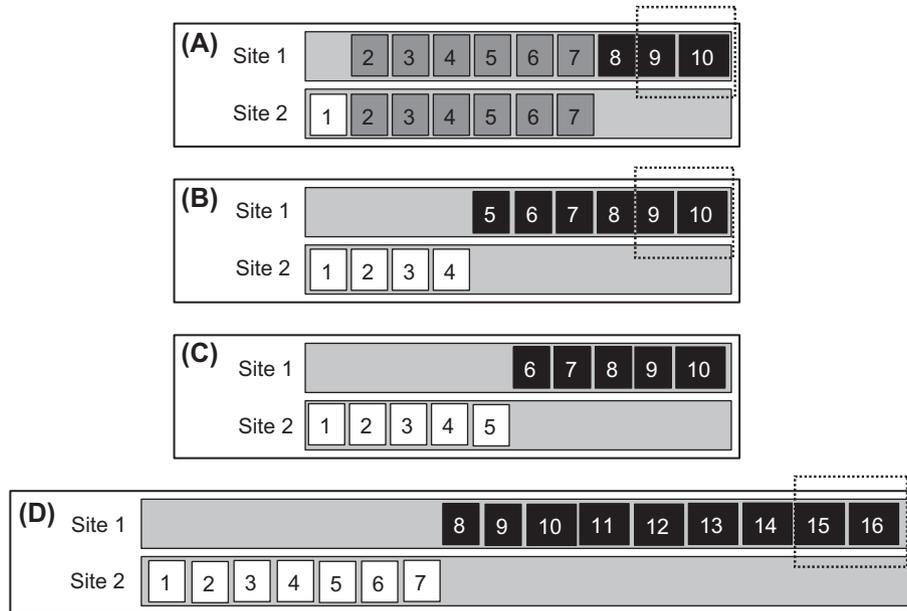
Figure 2. Comparison of possibilities for determining the theoretical upper limit of species replacement for a pair of sites (A) in which absolute species replacement is 2, the number of species shared is 6, and richness difference is 2. If the total number of species is kept constant, then the number of shared species may be divided equally, i.e. species 2–4 go to site 2, species 5–7 go to site 1, thus giving a value of 8 (B). The second possibility is splitting the set of shared species to compensate for richness differences, i.e. species 2–5 go to site 2 and species 6–7 go to site 1, yielding 10 (C). We may also assume that site totals remain fixed, so that the total number of species raises to 16, yielding a maximum replacement value of 14 (D). Black: species unique to site 1, white: species unique to site 2, dark gray: shared species. Dotted boxes enclose species responsible for richness difference.

In conclusion, measurement of replacement separately and measurement of the contribution of replacement to some other measure in Baselga's (2010, 2012) proposals are contradicting and, even if a separate coefficient is sought, the proposed formula does not satisfy the requirements set up by its own proponent.

Decomposition of beta diversity in the absence of nestedness

Now we examine the deduction that in absence of nestedness, i.e. when the nestedness resultant component is zero ($a = 0$), both total beta diversity and its replacement component take the value of 1, no matter whether Sørensen or Jaccard dissimilarity is partitioned. Baselga (2010, 2012) overlooked the fact that beta diversity is not always identical to species replacement if nestedness is lacking. We demonstrate this by the following three examples for site pairs j and k:

(a)		(b)		(c)	
j	k	j	k	j	k
1	0	1	0	1	0
0	1	1	0	1	0
0	1	1	0	1	0
0	1	0	1	1	0
0	1	0	1	0	1
0	1	0	1	0	1
0	1	0	1	0	1
0	1	0	1	0	1

In all cases, $\beta_{sor} = \beta_{sim} = 1$ as well as $\beta_{cc} = \beta_{jtu} = 1$. However, in absolute terms beta diversity is dominated by richness difference in (a) (1 species replaced by another but k has six other species), richness difference and species replacement are more balanced in (b) (3 species are replaced by other 3 and k has two more species than j) and, finally, richness difference is eliminated in (c) (both j and k have 4 species). That is, whenever $(b \neq c) > 0$ and $a = 0$, absolute beta diversity will have a fraction due to species replacement (i.e. $2\min(b, c)$) and another due to richness difference ($|b - c|$), and so will do relativized beta diversity. Beta diversity can be equated with species replacement only if $b = c$. Clearly, the indeterminate relationship persists even if $a > 0$. The conclusion is that the measure of beta diversity and its replacement component should carefully be selected and that β_{sim} and β_{jtu} as defined in Baselga (2010, 2012, respectively) do not reflect properly the replacement component of beta diversity quantified in either way, therefore β_{nes} and β_{jne} are meaningless. This basic problem of Baselga's methods is illustrated in the small example of Fig. 3. β_{nes} and β_{jne} reveal a hump-shaped relationship with increasing dissimilarity due to the loss of species and, hence, their behaviour is not consistent with the concept that they try to express quantitatively.

To sum it up, if $a = 0$ and $(b \neq c) > 0$ then beta diversity can still be partitioned into a replacement and a richness difference component and these component names are also valid, though nestedness does not exist. The conclusion is that even if beta diversity and the replacement component are properly selected, it is incorrect to call their difference as 'nestedness resultant component', because nestedness does not necessarily exist when that difference is larger than zero. Therefore, the ecologically meaningful term for this
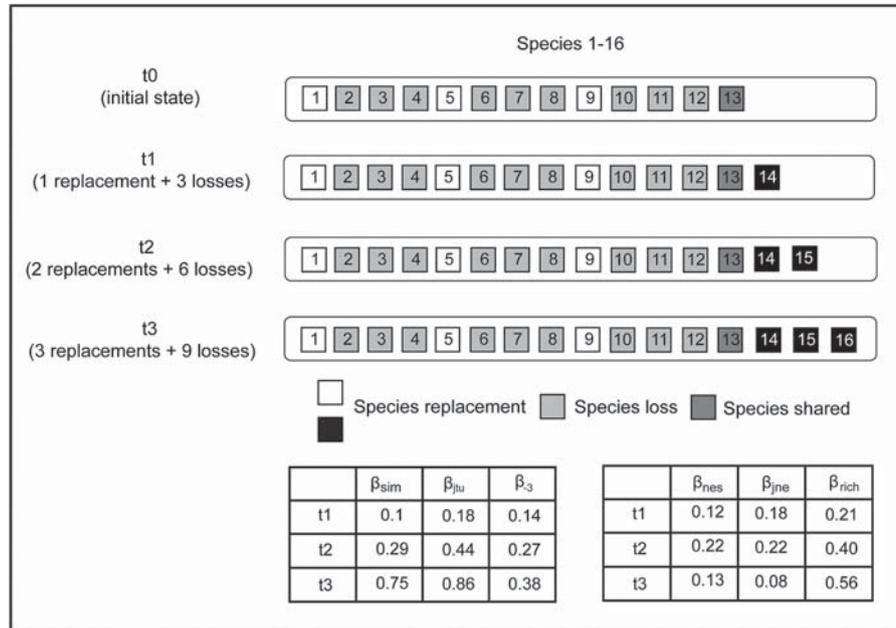
Figure 3. Simulation of a process of local extinctions in one site through time. Measures of dissimilarity were calculated for three time steps (t1, t2 and t3) in comparison with an initial state (t0). At each time step, one replacement (two species involved) and three losses occurred, totalling three replacements and 9 losses at the final stage (t3). Note that $\beta_{sim} > \beta_{nes}$ and $\beta_{jtu} > \beta_{jne}$, while $\beta_{-3} < \beta_{rich}$, when the loss of species is maximum and only three replacements had occurred (t3) and the humped-shaped response of β_{nes} and β_{jne} to the loss of species.

difference is 'richness difference', a term suggested independently by Podani and Schmera (2011) and Carvalho et al. (2012).

Testing the performance of different frameworks

The performance of the different frameworks for decomposing beta diversity into additive components was tested by a simulation study in which different gradients of dissimilarity, with known degrees of species replacement and species loss, were created. We also examined the behaviour of the different frameworks in the analysis of empirical data.

A simulation study

We created three artificial data sets modelling the temporal change of a given community under different conditions. Each community initially had 100 species. At each time step, each community suffered a predefined level of species replacement and species loss, according to three scenarios. In scenario 1, we increased the number of replacements and the number of losses by one at each step, therefore, species replacement > species loss (recall that one replacement involves two species). In scenario 2, the number of replacements was set to one, while the number of losses was set to two, hence species replacement = species loss. For scenario 3, the number of replacements was set to one and the number of losses was set to three, thus species replacement < species loss. We continued these processes for 25 steps in time. For each data set, beta diversity measures were calculated at each step in comparison to the initial state. Fig. 3 exemplifies the design of these simulations.

We advocate that an ecologically meaningful partitioning of beta diversity should obey two basic expectations under the simulated conditions: 1) any dissimilarity measure should increase monotonically in each scenario, because total dissimilarity, species replacement and species loss increase at every time step; 2) the ordering relationship between the measures deemed to represent species replacement (β_{sim}, β_{jtu} and β_{-3}) and species loss (β_{nes}, β_{jne} and β_{rich}) should be consistent with the proportion between the actual number of replacements and species losses in the three scenarios. These are the most intuitive and uncontroversial expectations that we can find. Any measure that does not satisfy these criteria would lead to obviously wrong ecological conclusions and conservation decisions.

All calculations were performed in the R statistical environment (R Development Core Team). The algorithm for the simulation and the calculation of all measures of beta diversity can be found in Supplementary material Appendix A1.

The results of simulations reveal different behaviours of the beta diversity partitioning methods (Fig. 4). Two functions, β_{nes} and β_{jne}, failed to satisfy the first requirement. These measures exhibited a hump-shaped behaviour along with increasing loss of species, meaning that when the loss of species is maximum, both measures give lower values than when losses are intermediate. Regarding the second criterion, all the measures seem to be consistent in scenario 1. For scenario 2, $\beta_{sim} > \beta_{jne}$ and $\beta_{jtu} > \beta_{jne}$ even though the level of replacements equals the level of losses at each time step. The performance of β_{jtu} and β_{jne} is even worse in scenario 3. In this case, a clear process of local extinction (species replacement < species loss) would be regarded by Baselga's framework as a process of
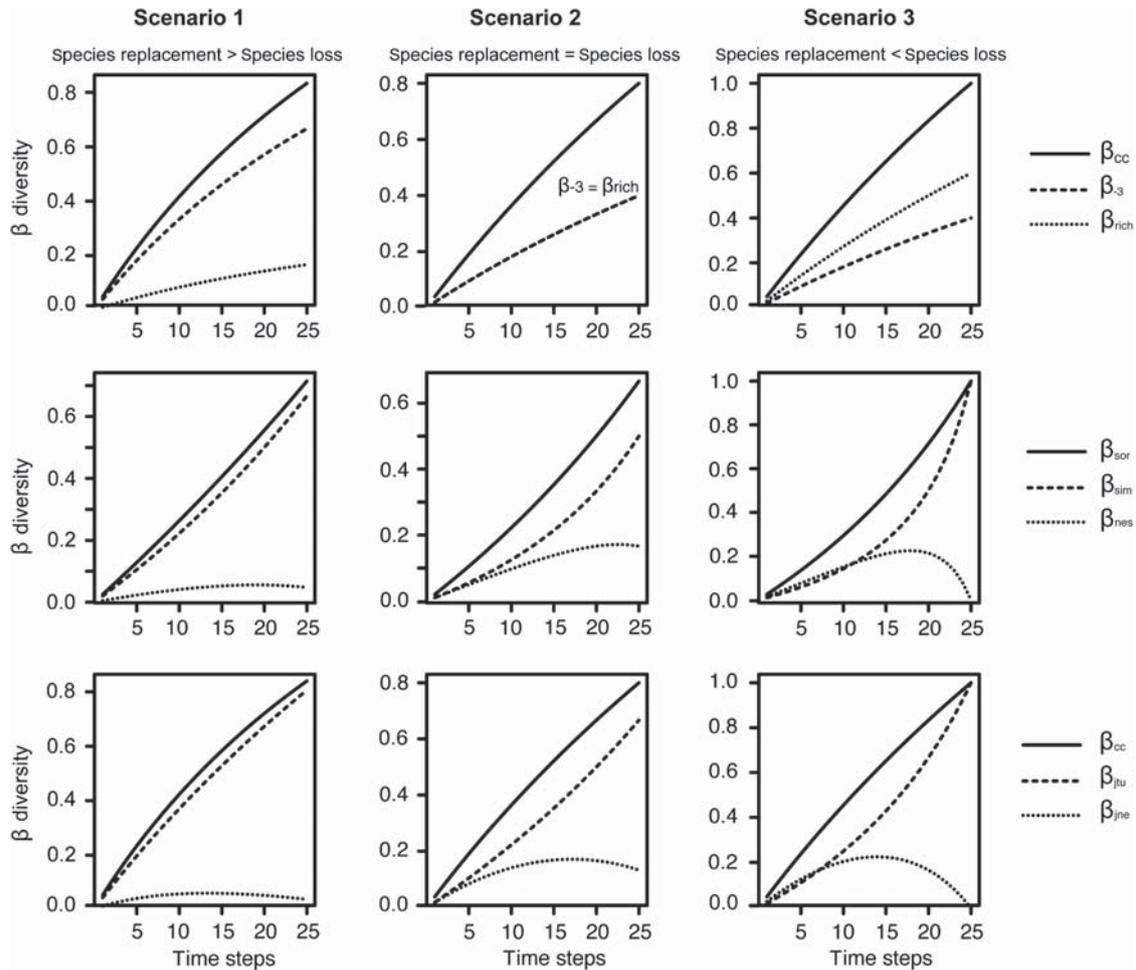
Figure 4. Response of β_{sim}, β_{nes}, β_{jtu}, β_{jne}, β_{-3}, β_{rich} in three simulated scenarios of increasing levels of species replacement and species loss along 25 time steps. In scenario 1, the number of replacements and the number of losses were set to one at each step, since one replacement involves two species, then species replacement > species loss. In scenario 2, the number of replacements was set to one, while the number of losses was set to two at each step, hence species replacement = species loss. For scenario 3, the number of replacements was set to one and the number of losses was set to three at each step, thus species replacement < species loss.

replacement ($\beta_{sim} > \beta_{jne}$ and $\beta_{jtu} > \beta_{jne}$). Moreover, when the last common species disappears, in spite of richness differences, there is no longer dissimilarity due to loss of species at all ($\beta_{nes} = 0$ and $\beta_{jtu} = 0$) and suddenly disimilarity is entirely due to species replacement ($\beta_{sim} = 1$ and $\beta_{jtu} = 1$). Therefore, we argue that in this case β_{nes} and β_{jtu} are consistent with the notion that two communities with no shared species could not be nested, but does not reflect the process (species loss) that originated this pattern. Contrary to β_{nes} and β_{jtu}, β_{rich} is proportional to the loss of species and reflects all richness differences, independently, of sites being nested or not (Fig. 4, scenario 3). In conclusion, only the performance of the partitioning of β_{cc} into β_{-3} and β_{rich} was consistent with the modelled gradients in all the three scenarios.

A case study

The islands of the Azorean archipelago suffered dramatic land-use changes since human occupation around 600 years ago (Triantis et al. 2010). Before human settlement, Azorean islands were mostly forested, but nowadays are dominated by highly modified habitats such as exotic

forests, semi-natural and intensive pastures, agricultural fields and orchards. Land-use change has influenced all taxonomic groups, in particular the arthropods, which are the richest of all taxa in the archipelago and also include the majority of endemic species (Borges et al. 2010). Moreover, their distribution is often very restricted, with many species responding at a fine spatial and temporal scale to habitat change (Borges et al. 2006, Cardoso et al. 2007, 2010, Triantis et al. 2010). Therefore, we can observe a predictably low level of species replacement and a high loss of endemic species, originating richness differences, from more natural to more disturbed land-use types due to selective local extinctions (Borges et al. 2008, Cardoso et al. 2009b, 2010, Fattorini et al. 2012). To test the different beta diversity partitioning methods under this scenario we sampled four land-use types corresponding to a gradient of increasing human induced changes in Terceira Island: native forest (dominated by *Laurus–Ilex*, *Juniperus* and *Erica* type forests), exotic forest (*Cryptomeria japonica* and *Eucalyptus* spp.), semi-natural pasture (located above 400 m and with the grazing concentrated in the summer months) and intensively managed pasture (grazed usually

all year) (details in Borges et al. 2008, Cardoso et al. 2009b). For each land-use type, eight sites were surveyed, following a standard procedure (Borges et al. 2005). Briefly, at each site a 150 m long transect was used to capture epigaeic fauna by pitfall trapping (30 traps distributed at 5 m intervals). The majority of arthropods (except Crustacea, Acari, Collembola, Hymenoptera and Diptera) were identified to species level.

The number of endemic species caught per sampling site decreases from native forest (mean = 7.8; SD = 3.1) to intensive pastures (mean = 2.6; SD = 0.9), exotic forest (mean = 1.9; SD = 1.7) and semi-natural pastures (mean = 1.6; SD = 1.4). Therefore, an ecologically meaningful partitioning of beta-diversity should reflect the selective extinction of endemic species into its richness differences component (or nestedness component, sensu Baselga 2010). Moreover, as very few endemic species mostly occur in disturbed habitats (Cardoso et al. 2009b, Fattorini et al. 2012), some replacement could also be expected, even if replacement is predictably lower than extinction. Four sampling sites were excluded from subsequent analysis because no endemic species were captured (two transects in exotic forest and two others in intensive pastures). We constructed a site × species matrix with the endemic species and subjected it to beta diversity partitioning analysis using the different frameworks. We used the non-parametric multivariate analysis of variance method (Anderson 2001) to test the null hypothesis of no differences of species replacement and richness differences among the four land-use types. This method compares the variance between groups with the variance within groups for a dissimilarity matrix by means of the sum of squared distances. The F-ratio was calculated, as in a single factor ANOVA model, and its p-value was obtained by 999 permutations. This procedure is implemented in the function 'adonis' of the vegan package (Oksanen et al. 2011) for the R environment (R Development Core Team).

Via partitioning β_{cc} into β_{-3} and β_{rich}, as expected, we could reject the null hypothesis for species replacement (measured by β_{-3}) and richness differences (measured by β_{rich}) and concluded that there was a significant difference across the four land-use types for both components of beta diversity. It is worth noting that R^2 for β_{rich} is higher than for β_{-3} indicating that the process of species loss (originating richness differences) is more important than the species replacement process (Table 2). Using the methods for partitioning β_{sor} into β_{sim} and β_{nes} or β_{cc} into β_{jtu} and β_{jne} (Baselga 2012, 2012), we rejected the null hypothesis for species replacement (measured by β_{sim} and β_{jtu}) but not the richness (nestedness) differences (measured by β_{nes} and β_{jne}) caused by the loss of species (Table 2). Therefore, we concluded that these frameworks failed to detect the local extinction process suffered by endemic species as a consequence of land-use changes. Thus, we argue that such frameworks may lead to wrong conclusions of conservation importance and land-use management strategies.

Discussion

A beta diversity partitioning method, in order to be ecologically meaningful, should reflect the processes that

Table 2. Non-parametric multivariate analysis of variance using β_{sim}, β_{nes}, β_{jtu}, β_{jne}, β_{-3}, β_{rich} for endemic arthropod communities sampled at four land-use types (DF – degrees of freedom, SS – sum of squares, MS – mean of squares, F – F-ratio, R^2 – explained variation, p – probability value obtained by 999 permutations).

	DF	SS	MS	F	R^2	p
β_{sim}						
Land-use	3	2.303	0.768	5.185	0.393	0.001
Residuals	24	3.553	0.148			
Total	27	5.856				
β_{nes}						
Land-use	3	0.248	0.083	2.641	0.248	0.120
Residuals	24	0.752	0.031			
Total	27	1.000				
β_{jtu}						
Land-use	3	2.498	0.833	4.416	0.356	0.001
Residuals	24	4.526	0.189			
Total	27	7.024				
β_{jne}						
Land-use	3	0.184	0.062	1.207	0.131	0.403
Residuals	24	1.222	0.051			
Total	27	1.407				
β_{-3}						
Land-use	3	0.704	0.235	2.370	0.229	0.045
Residuals	24	2.377	0.099			
Total	27	3.081				
β_{rich}						
Land-use	3	1.264	0.421	4.998	0.385	0.003
Residuals	24	2.023	0.084			
Total	27	3.287				

originate community variation, species replacement and species loss (or gain) and should reflect the proportional relationship between these two components (Williams 1996, Williams et al. 1999, Carvalho et al. 2012). In this paper, we addressed if the behaviour of three competing methods of beta diversity partitioning was consistent with these expectations.

Comparison of the three frameworks on theoretical grounds revealed three major, closely related problems in Baselga's (2010, 2012) methods. Most crucial is scaling, because the species replacement fractions (β_{sim} and β_{jtu}) are not standardized the same way as the overall dissimilarity measures (β_{sor} and β_{cc}, respectively) from which they are subtracted. In fact, the choice of the maximum possible values for such scaling is not substantiated because there are several other, equally if not more acceptable possibilities. The 'replacement' fraction of dissimilarity is ill-defined anyway for both cases because in the absence of nestedness beta diversity is not necessarily identical to replacement. In fact, β_{sim} does not represent the dissimilarity component of β_{sor} due to replacement, but represents the degree to which the species-poorer sampling unit is not nested within the species-richer sampling unit (Tuomisto 2010).

As a consequence, when tested against modelled gradients, the partitioning methods proposed by Baselga (2010, 2012) failed to accurately represent the species replacement and species loss processes that generate community variation. Moreover, when beta diversity was dominated by species losses, the measures of replacement (β_{sim} and β_{jtu}) were much higher than the measures of nestedness (β_{nes} and β_{jne}, deemed to represent the loss of species). Therefore, it

is now clear that these methods are inappropriate to infer the relative strengths of species replacement and species loss on the origins of community variation. We advocate that these methods could lead to irreversible conservation and management mistakes, for example, by erroneously identifying a particular area as a high replacement zone where in fact the process that is occurring is selective extinction, as in the case study presented in this paper.

To the contrary, the partition of β_{cc} into β_{-3} and β_{rich} consistently reflects the replacement and species loss (or gain) processes in generating beta diversity patterns, and showed a good proportional relationship between the two components when evaluated using model communities. Moreover, this framework clearly identified a pattern of endemic species loss associated to land-use changes in Terceira Island (Azores, Portugal). By decomposing beta diversity into its two sources of variation (species replacement and species richness differences) we demonstrated that community change was primarily determined by the loss of endemic species (originating richness differences among sites) from natural forests to exotic forests and semi-natural and intensive pastures. Before human settlement, forests occupied the entire island, therefore, the loss of endemic species seems to be caused by selective extinction as a consequence of species (in)tolerance to disturbance and land-use change (Borges et al. 2008, Cardoso et al. 2009b, 2010).

In conclusion, we advocate that any beta diversity measure should be evaluated by small artificial examples, simulated assemblages with well-defined properties and well-known empirical gradients in order to test whether its behaviour is consistent with the process that is supposed to be reflected. In the present case, we recommend the theoretically sound and algebraically correct decomposition of the Jaccard index, β_{cc} into β_{-3} and β_{rich}, when the objective of the study is to evaluate the relative roles of replacement and species loss (or gain) in generating beta diversity patterns. Baselga's approaches may appear interesting and attractive at first sight, but the methodological framework he uses is incoherent, his reasoning is often self-contradictory and therefore his procedures should be applied with much care.

References

Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. – Oikos 117: 1227–1239.

Almeida-Neto, M. et al. 2012. Rethinking the relationship between nestedness and beta diversity: a comment on Baselga (2010). – Global Ecol. Biogeogr. 21: 772–777.

Anderson, M. J. 2001. A new method for non-parametric multivariate analysis of variance. – Austral Ecol. 26: 32–46.

Anderson, M. J. et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. – Ecol. Lett. 14: 19–28.

Atmar, W. and Patterson, B. D. 1993. The measure of order and disorder in the distribution of species in fragmented habitat. – Oecologia 96: 373–382.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – Global Ecol. Biogeogr. 19: 134–143.

Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from nestedness and nestedness. – Global Ecol. Biogeogr. 19: 134–143.

Borges, P. A. V. et al. 2005. Ranking protected areas in the Azores using standardized sampling of soil epigean arthropods. – Biodivers. Conserv. 14: 2029–2060.

Borges, P. A. V. et al. 2006. Invasibility and species richness of island arthropods: a general model of endemic vs exotic species. – J. Biogeogr. 33: 169–187.

Borges, P. A. V. et al. 2008. Insect and spider rarity in an oceanic island (Terceira, Azores): true rare and pseudo-rare species. – In: Fattorini, S. (ed.), Insect ecology and conservation. Research Signpost, Kerala, India, pp. 47–70.

Borges, P. A. V. et al. 2010. A list of the terrestrial and marine biota from the Azores. – Príncipa Editora.

Cardoso, P. et al. 2007. Biotic integrity of the arthropod communities in the natural forests of Azores. – Biodivers. Conserv. 16: 2883–2901.

Cardoso, P. et al. 2009a. Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. – Divers. Distrib. 15: 1081–1090.

Cardoso, P. et al. 2009b. A spatial scale assessment of habitat effects on arthropod communities of an oceanic island. – Acta Oecol. 35: 590–597.

Cardoso, P. et al. 2010. Drivers of diversity in Macaronesian spiders and the role of species extinctions. – J. Biogeogr. 37: 1034–1046.

Carvalho, J. C. et al. 2012. Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns. – Global Ecol. Biogeogr. 21: 760–771.

Colwell, R. K. and Coddington, J. A. 1994. Estimating terrestrial biodiversity through extrapolation. – Phil. Trans. R. Soc. B 345: 101–118.

Fattorini, S. et al. 2012. Use of arthropod rarity for area prioritisation: insights from the Azorean islands. – PLoS One 7: e33995.

Harrison, S. et al. 1992. Beta diversity on geographic gradients in Britain. – J. Anim. Ecol. 61: 151–158.

Jaccard, P. 1912. The distribution of the flora in the alpine zone. – New Phytol. 11: 37–50.

Koleff, P. et al. 2003. Measuring beta diversity for presence–absence data. – J. Anim. Ecol. 72: 367–382.

Lennon, J. J. et al. 2001. The geographical structure of British bird distributions: diversity, spatial turnover and scale. – J. Anim. Ecol. 70: 966–979.

Melo, A. S. et al. 2009. Environmental drivers of beta diversity patterns in New World birds and mammals. – Ecography 32: 226–236.

Oksanen, J. et al. 2011. vegan: community ecology package. R package ver. 2.0-2. – < http://CRAN.R-project.org/package= vegan >.

Podani, J. and Schmera, D. 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence–absence data. – Oikos 120: 1625–1638.

Podani, J. and Schmera, D. 2012. A comparative evaluation of pairwise nestedness measures. – Ecography 35: 889–900.

Schmera, D. and Podani, J. 2011. Comments on separating components of beta diversity. – Comm. Ecol. 12: 153–160.

Simpson, G. G. 1943. Mammals and the nature of continents. – Am. J. Sci. 241: 1–31.

Sørensen, T. A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. – Kong. Danske Videnskabernes Selskabs Biol. Skr. 5: 1–34.

Triantis, K. A. et al. 2010. The Macaronesian province: patterns of species richness and endemism of arthropods. – In: Serrano, A. R. M. (ed.), Terrestrial arthropods of Macaronesia – biodiversity, ecology and evolution. Soc. Portuguesa Entomol., Lisbon, pp. 49–71.

Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. – Ecography 33: 23–45.

Ulrich, W. et al. 2009. A consumer's guide to nestedness analysis. – Oikos 118: 3–17.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – Ecol. Monogr. 30: 280–338.

Williams, P. H. 1996. Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. – Proc. R. Soc. B 263: 579–588.

Williams, P. H. et al. 1999. Interpreting biogeographical boundaries among Afro-tropical birds: spatial patterns in richness gradients and species replacement. – J. Biogeogr. 26: 459–474.

Supplementary material (available as Appendix O20980 at < www.oikosoffice.lu.se/appendix >). Appendix A1.