Determining the relative roles of species replacement and species richness differences in generating beta-diversity patterns

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ABSTRACT

Aim To determine the relative contribution of species replacement and species richness differences to the emergence of beta-diversity patterns.

Innovation A novel method that disentangles all compositional differences (β_{cc}, overall beta diversity) in its two components, species replacement (β_{-3}) and species richness differences (β_{rich}) is proposed. The performance of the method was studied with ternary plots, which allow visualization of the influence of the relative proportions of shared and unique species of two sites over each metric. The method was also tested in different hypothetical gradients and with real datasets. The novel method was compared with a previous proposal based on the partitioning of overall compositional differences (β_{sor}) in replacement (β_{sim}) and nestedness (β_{nes}). The linear response of β_{cc} contrasts with the curvilinear response of β_{sor} to linear gradients of dissimilarity. When two sites did not share any species, β_{sim} was always 1 and β_{-3} only reached 1 when the number of exclusive species of both sites was equal. β_{-3} remained constant along gradients of richness differences with constant replacement, while β_{sim} decreased. β_{rich} had a linear response to a linear gradient of richness differences with constant species replacement, whereas β_{nes} exhibited a hump-shaped response. Moreover, $\beta_{sim} > \beta_{nes}$ when clearly almost all species of one site were lost, whereas $\beta_{-3} < \beta_{rich}$ in the same circumstances.

Main conclusions The behaviour of the partition of β_{cc} into β_{-3} and β_{rich} is consistent with the variation of replacement and richness differences. The partitioning of β_{sor} into β_{sim} and β_{nes} overestimates the replacement component and underestimates richness differences. The novel methodology allows the discrimination of different causes of beta-diversity patterns along latitudinal, biogeographic or ecological gradients, by estimating correctly the relative contributions of replacement and richness differences.

Keywords
Diversity partitioning, nestedness, richness gradient, similarity indices, species loss, species replacement.

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INTRODUCTION

The study of beta-diversity patterns is one of the most fundamental issues in biogeography, ecology and conservation. Beta diversity was first defined as the extent of change in community composition along gradients (Whittaker, 1960). Since then, the term has been used to refer to a variety of phenomena, although all of these encompass some kind of compositional heterogeneity or differentiation between sites (for a revision see Tuomisto, 2010a,b, and Anderson *et al.*, 2011). Irrespective of the beta-diversity variant that is being used, two distinct processes shape communities and their differences: species substitution and species loss (or gain) (Williams, 1996; Williams *et al.*, 1999; Lennon *et al.*, 2001; Baselga, 2007, 2010).

The substitution of species in one site by different species in other site results in species replacement, while species loss (or gain) results in richness differences between sites. The mechanisms that contribute to species loss or gain are numerous; for example, selective extinction, colonization or dispersal limitation (Novotny & Weiblen, 2005; Urban *et al.*, 2006; Ulrich *et al.*, 2009). When such richness differences occur in an ordered manner along a gradient, smaller assemblages become subsets of larger ones and a nested pattern emerges (Atmar & Patterson, 1993). Therefore, nestedness can be regarded as a special case of an ordered pattern of differences in species richness. Most frequently, species replacement and richness differences occur along gradients in different proportions, giving rise to complex patterns of beta diversity. Disentangling the contribution of these two components of beta-diversity patterns is fundamental to understanding how communities react to spatial, environmental and temporal changes.

A considerable number of approaches have been used to study beta-diversity patterns (Magurran, 2004; Legendre *et al.*, 2005). One of the most popular methods is to conceive beta diversity as a measure of dissimilarity between sites. These measures can be classified into two groups, 'broad sense' measures, which incorporate differences in composition attributable to replacement and species richness differences, and 'narrow sense' measures that focus only on replacement (Koleff *et al.*, 2003). Several authors have compared both kinds of measures to gain insight into the mechanisms that generate beta-diversity patterns (Harrison *et al.*, 1992; Williams, 1996; Lennon *et al.*, 2001). However, none of these works established a comprehensive framework intended to disentangle the relative roles of species replacement and species richness differences in generating beta-diversity patterns.

Recently, a new method has been proposed to partition beta diversity into two components: replacement and nestedness (Baselga, 2010). This method was presented for pairwise and multiple-site comparisons. In the pairwise situation, an index of beta diversity due to nestedness (β_{nes}), which is deemed to represent richness differences among nested communities, is calculated by subtracting β_{sim} (replacement) from β_{sor} (overall beta diversity). The same rationale was used in multiple-site comparisons, using the multiple-site versions of β_{sor}, β_{sim} and β_{nes}. However, we advocate that this framework needs to be further tested with theoretical datasets representing different gradients of composition dissimilarity in order to evaluate its performance. Moreover, β_{sim} measure used in Baselga's (2010) approach actually overestimates replacement, as we show later in this paper.

Partitioning overall beta diversity into its replacement and nestedness components may not be the most obvious procedure, as nestedness is nothing more than a particular case of a species richness gradient. It seems more useful and intuitive to understand the nature of a particular beta-diversity pattern by partitioning it into its replacement and richness difference components, whether the community is nested or not. Therefore, we develop a novel and comprehensive framework intended to disentangle the relative roles of species
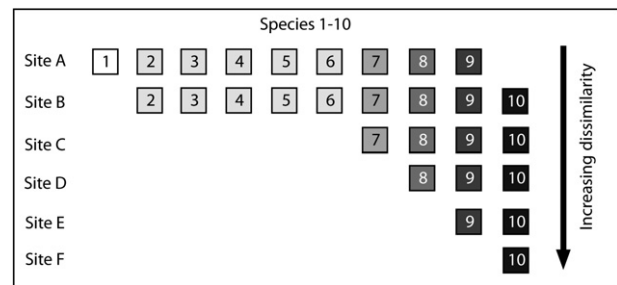
Figure 1 Hypothetical gradient of increasing dissimilarity. Sites A and B have the same richness but species 1 was replaced by species 10. Sites A, C, D, E differ in species richness and have at least one species in common (nested biotas). Sites A and F differ in species richness but do not share any species (non-nested biotas).

replacement and richness differences in generating beta-diversity patterns.

The performance of the novel framework was evaluated and compared with the previous proposal of Baselga (2010). For that purpose, the behaviour of the different measures was analysed with ternary plots, which allow visualization of the influence of the relative proportions of shared and exclusive species of two sites on the values of the different metrics (Koleff *et al.*, 2003). Moreover, four test cases representing different theoretical gradients of replacement and richness differences were constructed to evaluate the performance of both frameworks. Finally, we present two empirical datasets to demonstrate the usefulness and versatility of the framework proposed here in real scenarios.

INNOVATION

A novel method of partitioning beta diversity into species replacement and richness differences

Since we are interested in determining the relative roles of species replacement and richness differences in generating beta-diversity patterns we will use the term 'beta diversity' to refer all compositional changes between two sites irrespective of the process that originated it, in accordance with the original idea of Whittaker (1960). In the context of pairwise comparisons, a replacement occurs when one species is substituted by another species. For example, in Fig. 1, species 1 in site A is replaced by species 10 in site B. The expression 'richness differences' will be used to refer to the absolute difference between the number of species that each site contains, irrespective of being nested (site A and sites C, D and E, Fig. 1) or not (site A and site F, Fig. 1).

Therefore, beta diversity can be defined, mathematically, in relation to its two possible components as:

$$\text{beta diversity} = \text{replacement} + \text{richness differences.}$$

In order to derive the measures that should represent the three terms of the equation, we use the following standard notation (Koleff *et al.*, 2003): *a* is the number of species common to

Species 1-7

Site A   [1] [2] [3]   [4] [5]

Site B   [4] [5]   [6] [7]

         b   a   c
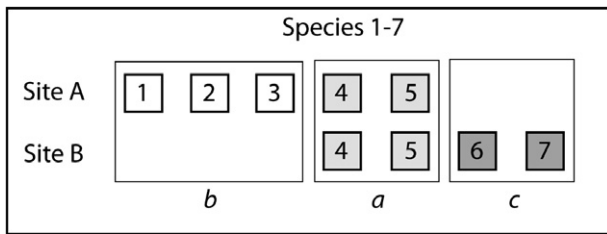
Figure 2 Matching/mismatching components between two sites: *a* is the number of shared species, *b* and *c* are the species exclusive to each site. The total number of species in the system is given by the sum *a* + *b* + *c*. The number of compositional differences between the two sites (total beta diversity) is given by the sum *b* + *c*. Richness difference is given by the absolute value of *b*–*c*. Replacement is given by min(*b*,*c*) multiplied by 2 (one substitution involves two species).

both sites, *b* is the number of species exclusive to the first site, and *c* is the number of species exclusive to the second site (Fig. 2). Therefore, the total compositional difference between two sites, independent of the process that originated it (replacement or richness differences), is given by the expression *b* + *c*. It is useful to think of compositional differences between two sites in the form of the proportion of these differences in relation to the total number of species recorded (*a* + *b* + *c*). Therefore, we obtain the Jaccard dissimilarity measure, also known as the β_{cc} complementarity measure of Colwell & Coddington (1994):

$$\beta_{cc} = \frac{b+c}{a+b+c}.$$

Conceptually, this approach corresponds to the variant of beta diversity defined as 'proportional effective species turnover' (Tuomisto, 2010a,b).

Replacement between two sites is the substitution of *n* species in a given site from *n* species in another site. Therefore, the number of substitutions between two sites is given by the minimum number of exclusive species, min(*b*,*c*), and the number of species involved in this process is 2 × min(*b*,*c*), since one substitution always involves two species. By expressing this quantity in the form of a proportion to the total number of species recorded (*a* + *b* + *c*), we obtain the measure β_{-3} of Williams (1996) as modified by Cardoso *et al.* (2009):

$$\beta_{-3} = 2 \times \frac{\min(b,c)}{a+b+c}.$$

The species richness of each site is given by the expressions *b* + *a* and *c* + *a*. Therefore, the absolute difference in species richness between two sites, expressed as a proportion of the total number of species recorded (*a* + *b* + *c*), is given by a new measure, which we designate as β_{rich}:

$$\beta_{rich} = \frac{|(b+a)-(c+a)|}{a+b+c} = \frac{|b-c|}{a+b+c}.$$

In conclusion, we postulate that beta diversity can be partitioned into two additive components, replacement and richness differences, according to the equation:

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

Related methods previously proposed

β_{rich} is in some way similar to the previously proposed β_{gl} (Lennon *et al.*, 2001), the only measure of species richness difference to date:

$$\beta_{gl} = \frac{2|b-c|}{2a+b+c}$$

Both measures differ in the fact that β_{gl} double-weights the absolute richness difference (numerator) and the shared species component. This does not allow the richness differences value to be expressed as a simple proportion of the total number of species recorded (*a* + *b* + *c*), a very useful and intuitive property of β_{rich}.

As we will extensively compare our novel method with the recent proposal of Baselga (2010), the only general framework proposed to date for partitioning beta diversity in its different components, we also represent this method. Baselga's framework can be represented by the equation:

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

β_{sor} is deemed to represent all compositional differences, i.e. overall beta diversity. In the dissimilarity form the index can be formulated as (Sørensen, 1948):

$$\beta_{sor} = \frac{b+c}{2a+b+c}.$$

β_{sor} is conceptually similar to β_{cc} by accounting for compositional differences (*b* + *c*). Both measures differ only because β_{sor} double-weights the shared species component. This means that β_{sor} expresses compositional differences in relation to the sum of species richness of both sites (usually larger than the total number of species recorded given that species may be shared).

β_{sim} is deemed to reflect compositional differences attributable to replacement. The index has the form (Lennon *et al.*, 2001):

$$\beta_{sim} = \frac{\min(b,c)}{a+\min(b,c)}.$$

It is worth noting that the numerator of β_{sim} expresses the number of substitutions, min(*b*,*c*), but not the number of species involved in the replacement process, 2 × min(*b*,*c*), between two sites. Apart from that, β_{sim} expresses the number of substitutions between two sites as a proportion to the number of species of the species-poorer site, unlike β_{sor} which expresses compositional differences as a proportion of the sum of species richness of both sites. This is non-trivial, because in this way the replacement in β_{sor} and the replacement in β_{sim} is not mathematically equivalent. Actually, β_{sim} is a measure of the proportion of the species-poorer site that is not nested in the species-

Table 1 Comparison of β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes} values along a hypothetical gradient of increasing dissimilarity (see Fig. 1 for details).

Sites	β_{cc}	β_{-3}	β_{rich}	β_{sor}	β_{sim}	β_{nes}
A–B	0.2	0.2	0	0.11	0.11	0
A–C	0.7	0.2	0.5	0.54	0.25	0.29
A–D	0.8	0.2	0.6	0.67	0.33	0.34
A–E	0.9	0.2	0.7	0.82	0.5	0.32
A–F	1	0.2	0.8	1	1	0

richer site (Tuomisto, 2010b). Therefore, β_{sim} overestimates replacement because it measures replacement relative to the species-poorer site and not as a proportion of all species.

β_{nes} is deemed to account for dissimilarity due to nestedness (Baselga, 2010). The index is obtained by subtracting β_{sim} from β_{sor}:

$$\beta_{nes} = \beta_{sor} - \beta_{sim} = \frac{\max(b,c) - \min(b,c)}{2a + \max(b,c) + \min(b,c)} \times \frac{a}{a + \min(b,c)}$$

$$= \frac{|b-c|}{2a + b + c} \times \frac{a}{a + \min(b,c)}.$$

Mathematically, β_{nes} may be viewed as a richness difference measure (the first term of the product), multiplied by the proportion of the species-poorer site that is nested in the species-richer site (the second term of the product).

The hypothetical gradient of dissimilarity illustrated in Fig. 1 allows a first comparison of the performance of our novel partitioning method with Baselga's (Table 1). Apart from the similarity between β_{cc} and β_{sor}, the other measures have totally different behaviours. While β_{-3} remains constant, reflecting the constancy of the number of substitutions between site A and the other sites, β_{sim} increases with increasing richness differences, which is a counter-intuitive behaviour of a measure that is deemed to reflect replacement. While β_{rich} reflects all richness differences along the gradient, β_{nes} is null when the last shared species disappears: $\beta_{rich}(A,F) = 0.8$; $\beta_{nes}(A,F) = 0$. This is a conceptual difference between the two measures, β_{nes} only accounts for differences in richness when sites are nested, i.e. when sites have at least one common species $(a > 0)$, while β_{rich} reflects all richness differences independently of sites being nested or not. Apart from this difference, both measures try, in fact, to reflect richness differences when the sites shared at least one species $(a > 0)$.

It is worth noting that in the graphical example of Fig. 1 two paradoxical situations are apparent in the behaviour of β_{nes} (Table 1): (1) $\beta_{nes}(A,D) > \beta_{nes}(A,E)$, when in fact site E has one species less than site D; (2) $\beta_{sim}(A,D) > \beta_{nes}(A,D)$, when clearly almost all species were lost and only one substitution has occurred. The behaviour of both partitions suggests that more formal testing is necessary to fully evaluate their usefulness.

Mathematical comparison of measures

The mathematical behaviour of the different measures was studied with ternary plots, as recommended by Koleff *et al.*
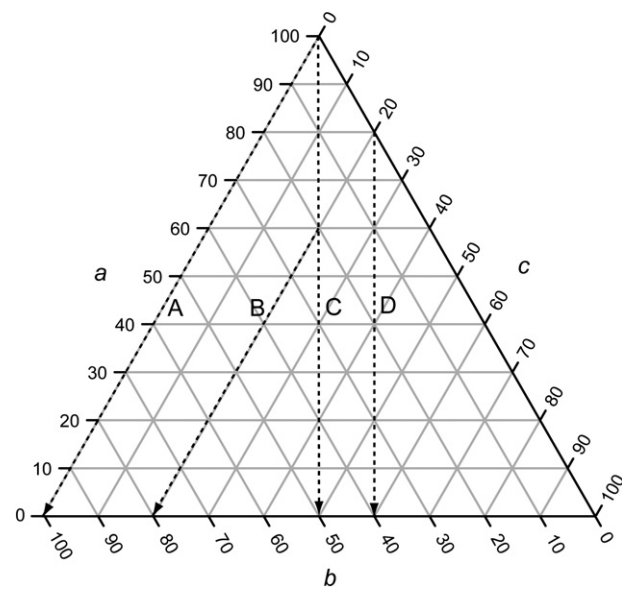
Figure 3 Ternary plot of the components *a*, *b* and *c* in the form of proportions: *a* is the proportion of the shared species between two sites; *b* and *c* are the proportions of the species exclusive to each site. Grey lines represent 10% increments of the components. Dashed lines represent four hypothetical gradients of richness differences and replacement: A, pure gradient of richness differences; B, mixed gradient of richness differences with a fixed constant replacement (20% of the species in the system); C, pure gradient of replacement; D, mixed gradient of replacement with constant richness differences (20% of the species in the system). The arrows represent the direction of increasing gradients.

(2003). Ternary plots allow visualization of the relationship between the matching/mismatching components (*a*, *b* and *c*), expressed as proportions, and the values of such measures, hence, $a + b + c = 100\%$ (Fig. 3). For that purpose, we used an artificial dataset with all possible combinations of the proportions of the components *a*, *b* and *c*, available in the simba package (Jurasinski, 2010) for the R statistical language (R Development Core Team, 2009).

Evaluating the performance of measures

To test the performance of the different measures and compare the novel method with the previous proposal by Baselga (2010), we constructed four test cases representing different gradients of known magnitude of replacement and richness differences. For the gradients to be independent of the variation in the overall number of species, the matching/mismatching components were expressed in the form of proportions, such that $a + b + c = 100\%$.

Test case 1. Pure gradient of richness differences

The number of substitutions was set to zero; hence one of the sites does not have any exclusive species $(c = 0\%)$. Therefore, richness differences increase linearly with decreasing values of

the *a* component and, conversely, increasing values of *b*. We advocate that measures of replacement should be null ($\beta_{-3} = \beta_{sim} = 0$), whereas measures of overall beta diversity (β_{cc} and β_{sor}) and richness differences (β_{rich} and β_{nes}) should decrease linearly with increasing values of the *a* component (Fig. 3, A).

Test case 2. Mixed gradient of richness differences with constant species replacement

The number of substitutions was set to a fixed known value (20% of the species in the system). Therefore, richness differences increase linearly with decreasing values of the *a* component and, conversely, increasing values of *b*. We advocate that measures of replacement (β_{-3} and β_{sim}) should be constant, whereas measures of overall beta diversity (β_{cc} and β_{sor}) and richness differences (β_{rich} and β_{nes}) should decrease linearly with increasing values of the *a* component (Fig. 3, B).

Test case 3. Pure gradient of species replacement

In this case richness differences were set to zero, hence $b = c$. Therefore, with decreasing values of the *a* component, *b* and *c* increase, and conversely, replacement increases linearly. We advocate that measures of richness differences should be null ($\beta_{rich} = \beta_{nes} = 0$), whereas measures of overall beta diversity (β_{cc} and β_{sor}) and replacement (β_{-3} and β_{sim}) should decrease linearly with increasing values of the *a* component (Fig. 3, C).

Test case 4. Mixed gradient of species replacement with constant richness differences

Richness difference was set to a fixed known value (20% of the species in the system), hence $|b - c| = $ constant (20%). Therefore, with decreasing values of the *a* component, *b* and *c* increase, and conversely, replacement increases linearly. We advocate that measures of richness differences (β_{rich} and β_{nes}) should be constant, whereas measures of overall beta diversity (β_{cc} and β_{sor}) and replacement (β_{-3} and β_{sim}) should decrease linearly with increasing values of the *a* component (Fig. 3 – D).

Values of the different measures (β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes}) were calculated and plotted against the shared species component (represented by the term *a* in all equations), in order to evaluate the performance of each index.

Disentangling beta-diversity patterns in replacement and differences of species richness in real scenarios

A small-scale example: response of spider assemblages to an ecological gradient

The response of spider assemblages to the invasion of coastal dunes by *Acacia* sp. was assessed using the framework proposed here. The study was carried out in the Amorosa dunes, northern Portugal (J.C. Carvalho, unpublished data). Three inventories of ground spiders were performed in three contrasting situations: coastal dunes with natural vegetation (control), coastal dunes

with low cover of *Acacia* sp. (< 50%) and coastal dunes with high cover of *Acacia* sp. (> 90%). Pairwise dissimilarity comparisons were performed among the three locations using β_{cc}, β_{-3} and β_{rich} metrics to evaluate the consequences of the invasion of an exotic plant species over the spider assemblages. A visual inspection of the spider assemblage composition of each site suggests that species loss increased with increasing *Acacia* sp. cover, resulting in high richness differences, although some species replacement also occurred (see Appendix S1 in Supporting Information). We expect that by partitioning β_{cc} into β_{-3} and β_{rich} the relative importance of species replacement and richness differences induced by the invasion of an exotic plant species on spider assemblages will be revealed. Specifically, with increasing cover of *Acacia* sp. the loss of species, represented by β_{rich}, should be greater than replacement, represented by β_{-3}. The partitioning of β_{sor} into β_{sim} and β_{nes} was also applied to this dataset in order to make a comparison with the partitioning of β_{cc} into β_{-3} and β_{rich}. All calculations were performed with the function 'betadiver' from the vegan package (Oksanen *et al.*, 2010) for the R statistical language (R Development Core Team, 2009).

A large-scale example: response of spider assemblages to a latitudinal/ biogeographic gradient

The dataset used in this example is fully described elsewhere (Carvalho *et al.*, 2011a,b). Basically, it consists of 18 standardized inventories carried out for coastal dunes along the western Atlantic coast of the Iberian Peninsula. The coast is almost perfectly aligned with the latitudinal axis and is dominated by a clear climatic gradient of mediterraneity from north to south, encompassing two biogeographic regions (Eurosiberian and Mediterranean).

To illustrate the behaviour of our method, we performed an analysis of biotic dissimilarity with geographic distance, which is the complement of distance-decay of similarity (Nekola & White, 1999), using β_{cc}, β_{-3} and β_{rich} as measures of dissimilarity. In this case, geographic distance corresponds to differences in latitude, since sampling sites were scattered along the latitudinal axis. Regressions were fitted in a log–log space to linearize the relationship between dissimilarity and distance. A Mantel test was applied to assess the significance of the relationship (Legendre & Legendre, 1998). All calculations were performed with the vegan package (Oksanen *et al.*, 2010) for the R statistical language (R Development Core Team, 2009). Spider species were divided into three groups, according to their origins: Mediterranean, non-Mediterranean and Iberian species (following Cardoso & Morano, 2010). Analyses were carried out independently for each group, to test the hypothesis that different processes act on spider assemblages depending on the biogeographic origins of the constituent species.

A visual inspection of the spider assemblage composition of each site suggests that the non-Mediterranean group suffers a process of species loss from north to south, resulting in high richness differences between northern and southern sites (see Appendix S2). This is expected since most non-Mediterranean species encounter in northern Iberia the southernmost limit of

their geographic distribution. On the contrary, in the Mediterranean and Iberian groups, replacement seems to be the dominant process. Therefore, for non-Mediterranean species, we predict that the slope of the distance–dissimilarity plot of β_{rich} (richness differences) should be higher than the slope of the distance–dissimilarity plot of β_{-3} (replacement). On the other hand, for Mediterranean and Iberian species, we predict that the slope of the distance–dissimilarity plot of β_{-3} (replacement) should be higher than the slope of the distance–dissimilarity plot of β_{rich} (richness differences). The partitioning of β_{sor} in β_{sim} and β_{nes} was also applied to this dataset in order to make a comparison with the partitioning of β_{cc} in β_{-3} and β_{rich}.

CASE STUDY RESULTS

Mathematical comparison of measures

The comparison of frameworks with ternary plots showed striking differences in their behaviour. In both partitioning methods,

β_{cc} and β_{sor} reflect overall beta diversity independently of the process that originated it. Both measures are similar, differing only in the fact that β_{sor} double-weights the a component. This difference has a significant effect on their performance. The magnitude of change of β_{cc} values is proportional to the magnitude of change of the a component. On the contrary, the changes of the values of β_{sor} are faster when the values of a are low (Fig. 4).

β_{-3} and β_{sim} are deemed to reflect replacement. The values of β_{-3} and β_{sim} are maximum when $b = c$ and $a = 0$. This is in conformity with the expected notion that species replacement is maximum when all the species of a given site are substituted by a different set with the same number of species. These measures differ in that β_{-3} is less sensitive than β_{sim} to small changes in b or c components when the a component and b or c are low. Since both measures are intended to reflect species replacement, this means that in this situation a small change in species replacement would yield a large change in β_{sim} values, while β_{-3} would change proportionally to the magnitude of that change.
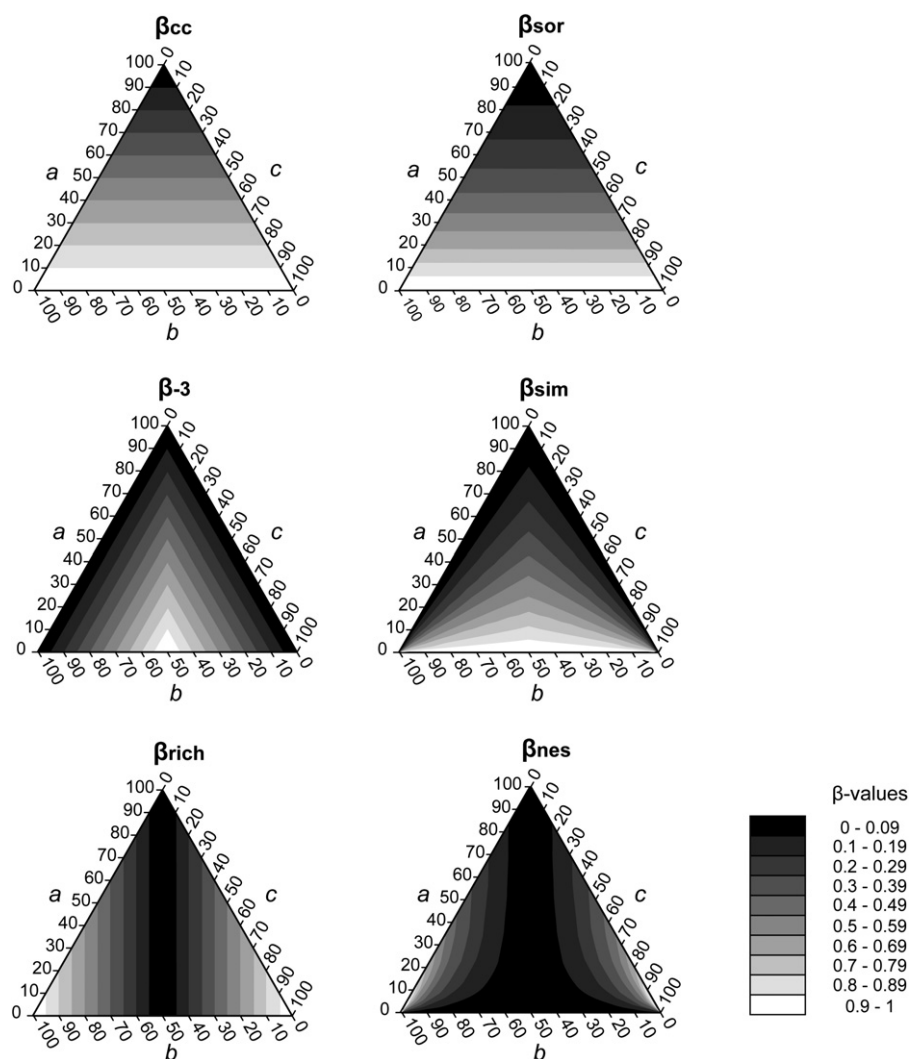
Figure 4 Ternary plots showing the variation of the values of β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes} for all possible combinations of the components a, b and c, expressed in the form of proportions, so that $a + b + c = 100\%$.
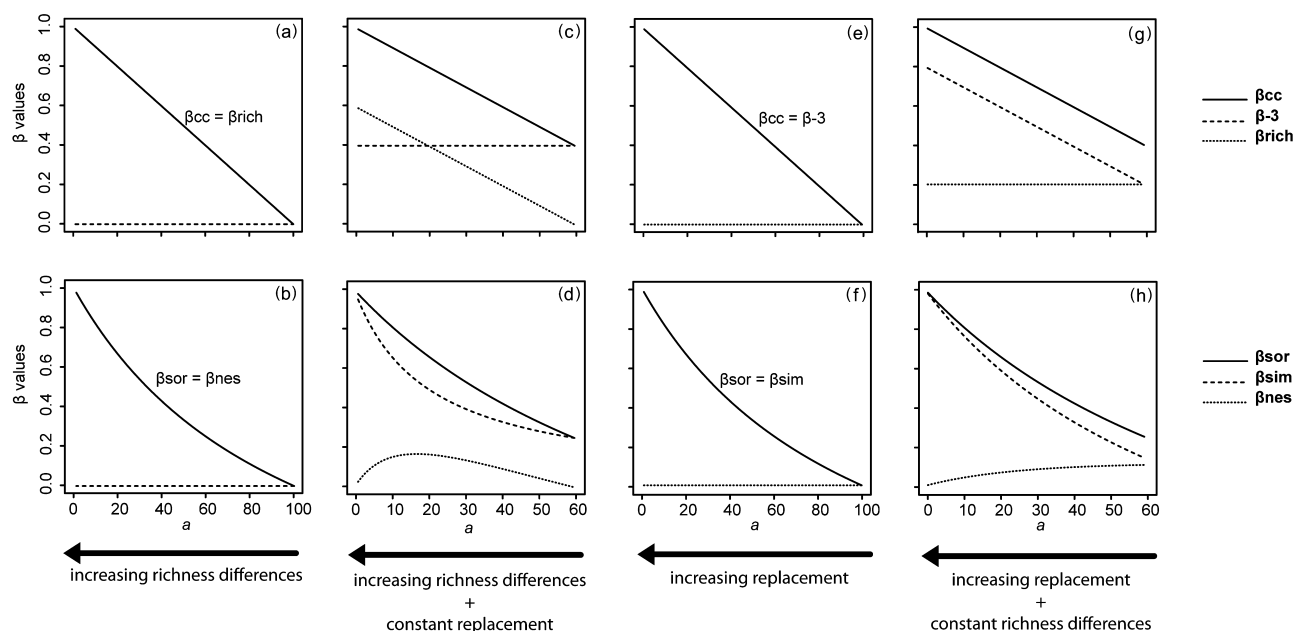
Figure 5 Response of β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes} measures to four linear gradients of replacement and richness differences: pure gradient of richness differences (a, b); mixed gradient of richness differences with constant replacement (20% of the species in the system) (c, d); pure gradient of replacement (e, f); mixed gradient of replacement with constant richness differences (20% of the species in the system) (g, h). The values of the measures were calculated for all possible combinations of the components *a*, *b* and *c*, expressed in the form of proportions, so that $a + b + c = 100\%$. Decreasing values of the component a represent increasing gradients.

Moreover, when $a = 0$, β_{sim} is always 1 and β_{-3} only reaches 1 when $b = c$ (Fig. 4).

β_{rich} and β_{nes} give a null value when $b = c$. In this situation, there are no richness differences, and compositional differences are due to replacement only. The two measures differ when two sites do not share any species ($a = 0$), β_{rich} is proportional to the species richness difference between them, while β_{nes} is always 0 (Fig. 4). Therefore, β_{rich} accounts for all richness differences, while β_{nes} accounts only for richness differences when $a > 0$.

Evaluating the performance of measures

Test case 1. Pure gradient of richness differences

In this scenario, both partitions exhibited a similar behaviour, differing only in the fact that β_{cc} and β_{rich} had a linear behaviour (Fig. 5a), whereas β_{sor} and β_{nes} responses were curvilinear (Fig. 5b). $\beta_{-3} = \beta_{sim} = 0$, according to the expectations.

Test case 2. Mixed gradient of richness differences with constant species replacement

Although β_{cc} and β_{sor} had a similar response, measures of replacement and richness differences of both partitions exhibited different behaviours. β_{-3} was constant (Fig. 5c) contrary to β_{sim} that diminished with increasing values of the shared component (Fig. 5d). β_{rich} decreased linearly with decreasing richness differences (Fig. 5c), contrary to β_{nes} that showed a hump-shaped response (Fig. 5d). This means that β_{nes} reached its

maximum value for an intermediate value of richness differences. Thus, β_{nes} reached minimum values, similarly, when richness differences were high (*a* near 0) and when richness differences were small (highest values of *a*). Moreover, the values of β_{-3} and β_{rich} have a good proportional relationship, contrary to β_{sim} and β_{nes}. In fact, $\beta_{sim} > \beta_{nes}$ when richness differences were high (*a* near 0), contrary to what one might intuitively expect. In such circumstances β_{sim} seems to overestimate replacement, while β_{nes} underestimates richness differences.

Test case 3. Pure gradient of species replacement

The values of β_{cc}, β_{-3}, β_{sor} and β_{sim} decreased with decreasing replacement, according to expectations, but β_{cc} and β_{-3} had linear responses to the linear gradient, contrary to β_{sor} and β_{sim} that were curvilinear. $\beta_{rich} = \beta_{nes} = 0$, according to expectations (Fig. 5e,f).

Test case 4. Mixed gradient of species replacement with constant richness differences

β_{cc} and β_{-3} decreased linearly with decreasing replacement (Fig. 5g), whereas the response of β_{sor} and β_{sim} was curvilinear (Fig. 5h). Although richness differences were constant along this gradient, β_{nes} varied, increasing towards a maximum value (Fig. 5h). β_{rich} was constant (Fig. 5g), according to expectations.

Table 2 Comparison of β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes} values of spider assemblages along a gradient of invasion of coastal dunes by *Acacia* sp.

	β_{cc}	β_{-3}	β_{rich}	β_{sor}	β_{sim}	β_{nes}
Control vs. low *Acacia* cover	0.51	0.24	0.27	0.35	0.20	0.15
Control vs. high *Acacia* cover	0.76	0.29	0.47	0.62	0.39	0.23
Low *Acacia* cover vs. high *Acacia* cover	0.50	0.18	0.32	0.33	0.15	0.18

Spiders were sampled in three sites: control, natural dune vegetation without *Acacia* sp.; low *Acacia* cover ($< 50\%$); high *Acacia* cover ($> 90\%$).

Disentangling beta-diversity patterns in replacement and differences in species richness for real scenarios

A small-scale example: response of spider assemblages to an ecological gradient

β_{cc} values indicate that compositional changes were relatively high (Table 2). By decomposing these values into β_{-3} and β_{rich} we find that in all possible pairwise comparisons, compositional differences attributable to richness differences were higher than compositional differences attributable to species replacement (Table 2). For example, for the pairwise comparison natural dune versus dune with high cover of *Acacia* sp., $\beta_{cc} = 0.76$, $\beta_{-3} = 0.29$ and $\beta_{rich} = 0.47$. Therefore, we may conclude that compositional differences determined by replacement accounted for 38% (β_{-3}/β_{cc}) and compositional differences determined by species loss accounted for 62% (β_{rich}/β_{cc}) of all compositional differences.

The partitioning of β_{sor} in β_{sim} and β_{nes} gives remarkably different results (Table 2). For example, for the pairwise comparison natural dune versus dune with high cover of *Acacia* sp., $\beta_{sor} = 0.62$, $\beta_{sim} = 0.39$ and $\beta_{rich} = 0.23$, thus indicating that compositional differences determined by replacement accounted for 63% (β_{sim}/β_{sor}) and compositional differences determined by species loss accounted for 37% (β_{nes}/β_{sor}). However, the visual inspection of the species composition of each site clearly suggests that species loss is much more important than replacement (see Appendix S1). Therefore, β_{nes} seems to underestimate the true loss of species, while β_{sim} appears to overestimate replacement.

A large-scale example: response of spider assemblages to a latitudinal/biogeographic gradient

Overall dissimilarity calculated with β_{cc} increased with geographic distance for the three groups of spiders, revealing the strong influence of the spatial gradient of mediterraneity on the assemblage structure of spiders (Fig. 6). Slopes and intercepts were identical, thus we may conclude that beta-diversity patterns among the three groups of spiders were similar (Table 3). However, by disentangling β_{cc} in its two components, replacement (β_{-3}) and richness differences (β_{rich}), we find that replacement was much more important for Mediterranean and Iberian

species than richness differences. On the contrary, beta diversity attributable to richness differences was more important in the non-Mediterranean spider species group than replacement. These results are consistent with our expectations given the composition of spider fauna of each site (see Appendix S2).

The partitioning of β_{sor} in β_{sim} and β_{nes} gives strikingly different results (Fig. 6). For the three groups of spiders the slopes of the distance–dissimilarity plot were always higher for β_{sim} than for β_{nes} (Table 3). Although the non-Mediterranean spider group suffers a clear decline in richness from north to south (see Appendix S2), the slope of the distance–dissimilarity plot of β_{nes} for this group was remarkably low (Table 3). Therefore, this framework failed to detect the process of species loss suffered by the non-Mediterranean spider species group.

DISCUSSION

Beta diversity can be conceptualized as the change in community structure along a gradient (turnover) or the variation in community structure among sampling units within a given area without reference to a particular gradient or direction (Anderson *et al.*, 2011). Independently of the perspective, turnover versus variation, beta-diversity patterns are determined by two basic processes: the replacement of species and richness differences. Assessing the relative role of each component in determining beta-diversity patterns is a fundamental task in biogeography, ecology and conservation (Williams, 1996; Williams *et al.*, 1999; Baselga, 2007). We propose a novel method that disentangles all compositional differences (β_{cc}, overall beta diversity) into its two components, species replacement (β_{-3}) and species richness differences (β_{rich}). By accounting for the two components of beta diversity, this method allows us to study the turnover of species along directional gradients and the variation in community structure without reference to a particular gradient or direction (see Anderson *et al.*, 2011).

The novel approach is conceptually similar to the partitioning of β_{sor} into a replacement component (β_{sim}) and a nestedness component (β_{nes}), proposed by Baselga (2010). Both partitions differ conceptually in the fact that β_{rich} accounts for all richness differences whereas β_{nes} accounts for species richness differences due to nestedness (*sensu* Baselga, 2010). In practice, $\beta_{nes} = 0$ if two communities do not share any species ($a = 0$), independently of their richness differences, while β_{rich} reflects these differences. When sites share at least one species ($a > 0$), β_{nes} tries to measure their richness differences like β_{rich}. Therefore, both frameworks try to partition beta diversity into its two components: replacement and richness differences and, hence, their performance could be compared.

Performance

Both partitions were analysed with ternary plots (Koleff *et al.*, 2003) and tested against linear gradients of replacement and richness differences. We found that the partitioning of β_{cc} into
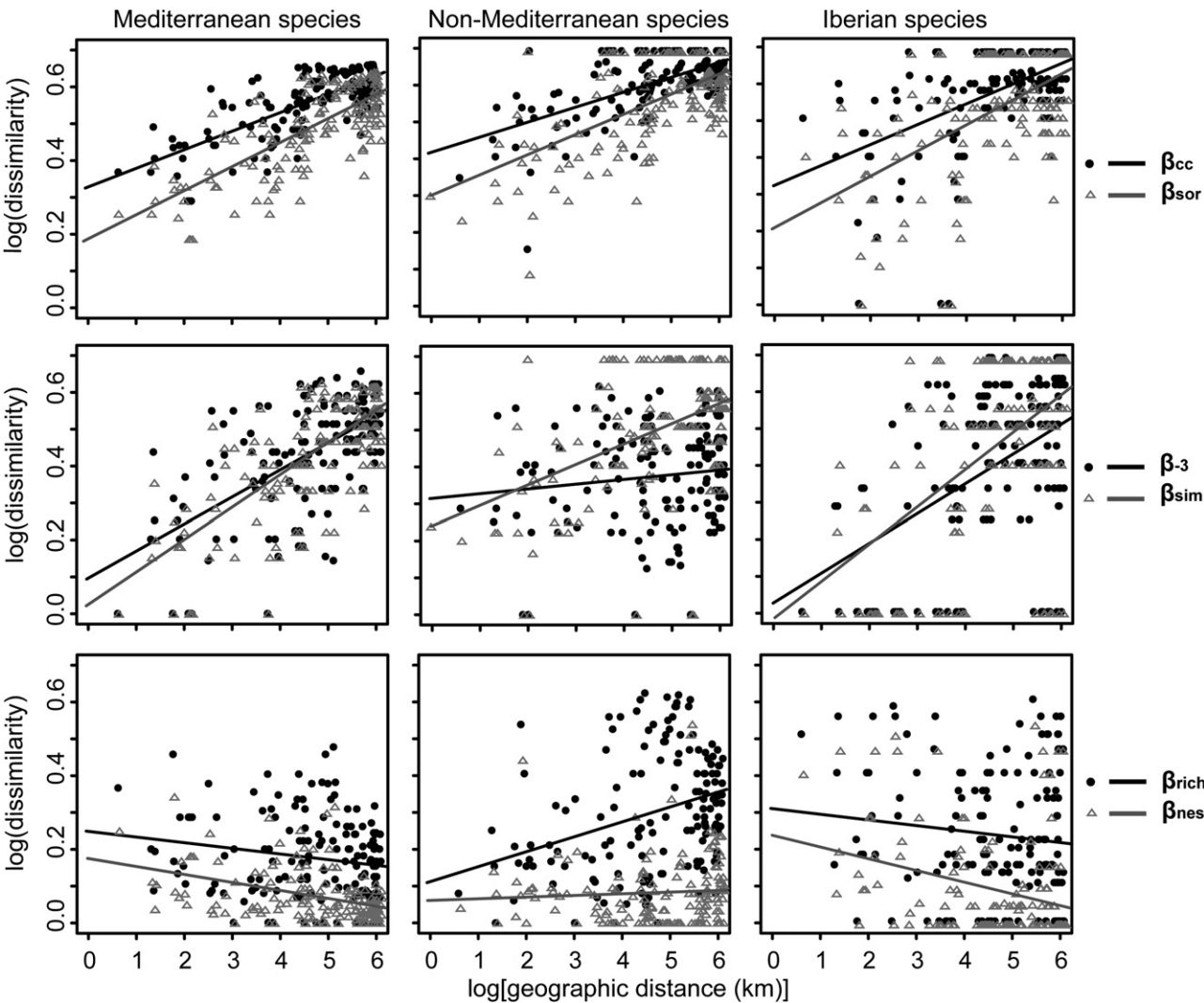
Figure 6 Relationship between spider assemblage dissimilarity and geographic distance. β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes} were used as measures of dissimilarity. Regressions were fitted in a log–log space to linearize the relationship between dissimilarity and distance.

Table 3 Results from ordinary least-squares regression of the β_{cc}, β_{-3}, β_{rich}, β_{sor}, β_{sim} and β_{nes}, by distance between pairs of 18 coastal dune sites.

Species origins	β_{cc}	β_{-3}	β_{rich}	β_{sor}	β_{sim}	β_{nes}
Mediterranean						
Intercept	0.327	0.097	0.248	0.183	0.026	0.172
Slope	0.051	0.073	−0.015	0.065	0.087	−0.021
Mantel *r*	0.755*	0.626*	−0.176*	0.746*	0.723*	−0.396*
Non-Mediterranean						
Intercept	0.421	0.321	0.113	0.302	0.243	0.060
Slope	0.040	0.012	0.041	0.055	0.055	0.004
Mantel *r*	0.623*	0.116[n.s.]	0.325*	0.604*	0.436*	0.063[n.s.]
Iberian						
Intercept	0.324	0.023	0.306	0.211	−0.017	0.237
Slope	0.056	0.081	−0.015	0.070	0.102	−0.032
Mantel *r*	0.543*	0.477*	−0.115*	0.557*	0.528*	−0.307*

Regression models were fitted in a log–log space and applied separately for Mediterranean, non-Mediterranean and Iberian spider species. A Mantel test was applied to assess the significance of the relationship of the Pearson correlation coefficient (*r*): *$P < 0.05$; n.s. not significant.

β_{-3} and β_{rich} was consistent with the variation of the degree of replacement and richness differences and showed linear responses to linear gradients of richness differences and replacement. We argue that linearity is an obligatory property, as it ensures that the magnitude of change in dissimilarity among sites is reflected by the measures employed to depict beta-diversity patterns. Moreover, many statistical methods demand linearity of dissimilarity measures (Legendre & Legendre, 1998). Complying with these properties, we advocate that partitioning of β_{cc} in β_{-3} and β_{rich} allows a correct estimation of the relative contribution of species replacement and richness differences to the emergence of beta-diversity patterns.

The partitioning of β_{sor} into β_{sim} and β_{nes} gave similar results to the partitioning of β_{cc} into β_{-3} and β_{rich} in pure gradients of richness differences and pure gradients of replacement, but exhibited a counter-intuitive behaviour along mixed gradients of richness differences and replacement. The response of β_{sim} and β_{nes} was inconsistent with the variation of replacement and richness differences in mixed gradients. The worse performance of Baselga's method seems to derive from a basic flaw: the replacement in β_{sim} is not mathematically equivalent to the replacement in β_{sor}. β_{sor} could be regard as a measure of all the compositional differences between two sites, thus including a component of replacement and a component of richness differences, expressed as a proportion of the sum of species richness values in both sites (contrary to β_{cc} which is expressed as a proportion of the total number of species in the system). Therefore, we advocate that an exact replacement partition of β_{sor} should be done in relation to the sum of species richness values in both sites. However, as Tuomisto (2010b) notes, β_{sim} quantifies the proportion of the species-poorer site that is not nested in the species-richer site, thus ignoring the number of species in the richer site. Therefore, β_{sim} can be regard as a measure of replacement in relation to the richness of the species-poorer site, but not to the richness of both sites. This often causes β_{sim} to overestimate the replacement component in mixed scenarios of replacement and richness differences. Since, β_{nes} was obtained by subtracting β_{sim} from β_{sor}, it tends to underestimate the richness differences component. These shortcomings may lead to misleading results and conclusions, as verified with the two empirical examples presented in this paper. Therefore, we argue that, although the idea of disentangling beta diversity in replacement and nestedness (*sensu* Baselga, 2010) is straightforward, the behaviour of the proposed metrics advises serious caution in their use.

Furthermore, our method presents the additional advantage of relying on measures robust to undersampling (Cardoso *et al.*, 2009). Therefore, relying on β_{cc}, β_{-3} and β_{rich} minimizes the under- or over-estimation of beta-diversity values due to comparisons of incomplete species lists. On the contrary, β_{sor} and β_{sim} are among the most sensitive metrics to undersampling (Cardoso *et al.*, 2009). Beta-diversity patterns could be biased due to comparisons of incomplete species lists, a common problem in invertebrate community studies among others (Novotny & Basset, 2000; Longino *et al.*, 2002; Coddington *et al.*, 2009).

Applications to real scenarios

This novel method was revealed to be useful and versatile in the study and understanding of real datasets differing in their nature (ecological versus biogeographic gradients) and scale (small versus large gradients). In the simplest case, the response of spider assemblages was studied along an invasion gradient of coastal dunes by *Acacia* sp. by using simple direct comparisons of the indices (β_{cc}, β_{-3} and β_{rich}). Striking changes in the composition of spider assemblages were found. By decomposing the overall beta diversity (β_{cc}) into its two sources, we find that differences in species richness were more important than replacement. Therefore, we conclude that the relative contribution of species loss to the observed pattern was more important than species replacement. Spiders are strongly affected by the physical features of their habitat, like humidity, temperature and vegetation structure (Uetz, 1991; Wise, 1993). The natural mosaic of open sand, moss, lichens, herbaceous plants and small shrubs was radically transformed by *Acacia* sp. into a dense shrub canopy with a blanket of dense foliage on the ground. Therefore, we suggest that changes in the physical structure of the litter/soil microhabitat with the invasion of *Acacia* sp. are the likely cause of the substantial loss of spider species.

In the large-scale study case, beta diversity of spider assemblages was studied along a latitudinal/biogeographic gradient of mediterraneity by using the complement of distance–decay plots of similarity, taking in account the biogeographic origins of spiders. For the Mediterranean and Iberian spider groups, replacement was the main process that determined compositional differences. This pattern is certainly determined by a combination of the climatic gradient of mediterraneity and historical processes, which favoured the replacement of species along the gradient. For example, the replacement of Iberian species is most probably a consequence of allopatric speciation events that occurred along the complex history of the Iberian Peninsula (Gómez & Lunt, 2007). On the contrary, non-Mediterranean species appear to suffer a sorting process along the latitudinal/climatic gradient of mediterraneity, resulting in the loss of species from north to south and, consequently, in richness differences among sites. Therefore we conclude that different processes act on spider assemblages along this large-scale gradient depending on the species biogeographic origins.

Using the new framework in multiple-site comparisons

The method proposed here is limited to pairwise comparisons. This could be appropriate when we want to evaluate (dis)similarity along a latitudinal or environmental gradient, as we demonstrate in the response of spider assemblages to a latitudinal/biogeographic gradient. However, we acknowledge that this is a shortcoming in multiple-site comparisons, i.e. when we want to compare three or more collections of sites from different regions (Diserud & Ødegaard, 2007). A possible way to overcome this limitation in multiple-site situations is to calculate the average of all pairwise dissimilarities for each region. As pairwise similari-

ties are not independent and they ignore the information on species shared among multiple sites (Diserud & Ødegaard, 2007), the development of a multiple-site similarity version of this method is nevertheless desirable, although it is beyond the scope of this paper.

Concluding remarks

In conclusion, the novel framework proposed here presents several interesting attributes: it is simple to apply and to understand, it is intuitive, the metrics used gave consistent responses to different test cases and are robust to undersampling, and it is versatile according to the nature and the scale of the study. By decomposing overall beta diversity into its two sources, replacement and richness differences, and by estimating their relative contributions, we ensure that the different causes of the observed patterns are discriminated and quantified. Thus, our framework provides a standard for comparisons of different sites and studies with different levels of species richness. We conclude that this method can contribute to describing and understanding the complexity of beta-diversity patterns that emerge along latitudinal, biogeographic or ecological gradients.

REFERENCES

Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C. & Swenson, N.G. (2011) Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, **14**, 19–28.

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

Baselga, A. (2007) Disentangling distance decay of similarity from richness gradients: response to Soininen *et al.* 2007. *Ecography*, **30**, 838–841.

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, **19**, 134–143.

Cardoso, P. & Morano, E. (2010) The Iberian spider checklist (Araneae). *Zootaxa*, **2495**, 1–52.

Cardoso, P., Borges, P.A.V. & Veech, J.A. (2009) Testing the performance of beta diversity measures based on incidence data: the robustness to undersampling. *Diversity and Distributions*, **15**, 1081–1090.

Carvalho, J.C., Cardoso, P., Crespo, L.C., Henriques, S., Carvalho, R. & Gomes, P. (2011a) Determinants of beta diversity of spiders in coastal dunes along a gradient of mediterraneity. *Diversity and Distributions*, **17**, 225–234.

Carvalho, J.C., Cardoso, P., Crespo, L.C., Henriques, S., Carvalho, R. & Gomes, P. (2011b) Determinants of spider species richness in coastal dunes along a gradient of mediterraneity. *Insect Conservation and Diversity*, doi: 10.1111/j.1752-4598.2011.00139.x.

Coddington, J.A., Agnarsson, I., Miller, J.A., Kuntner, M. & Hormiga, G. (2009) Undersampling bias: the null hypothesis for singleton species in tropical arthropod surveys. *Journal of Animal Ecology*, **78**, 573–584.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **345**, 101–118.

Diserud, O.H. & Ødegaard, F. (2007) A multiple-site similarity measure. *Biology Letters*, **3**, 20–22.

Gómez, A. & Lunt, D.H. (2007) Refugia within refugia: patterns of phylogeographic concordance in the Iberian Peninsula. *Phylogeography of southern European refugia* (ed. by S. Weiss and N. Ferrand), pp. 155–188. Springer, Dordrecht, The Netherlands.

Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta-diversity on geographic gradients in Britain. *Journal of Animal Ecology*, **61**, 151–158.

Jurasinski, G. (2010) Package 'simba': a collection of functions for similarity analysis of vegetation data. R package version 0.3-2. Available at: http://cran.r-project.org (accessed 1 September 2010).

Koleff, P., Gaston, K.J. & Lennon, J.K. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, **72**, 367–382.

Legendre, P. & Legendre, L. (1998) *Numerical ecology*, 2nd English edition. Elsevier Science BV, Amsterdam.

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, **75**, 435–450.

Lennon, J.J., Koleff, P., Greenwood, J.J.D. & Gaston, K.J. (2001) The geographical structure of British bird distributions: diversity, spatial turnover and scale. *Journal of Animal Ecology*, **70**, 966–979.

Longino, J.T., Coddington, J. & Colwell, R.K. (2002) The ant fauna of a tropical rain forest: estimating species richness three different ways. *Ecology*, **83**, 689–702.

Magurran, A.E. (2004) *Measuring biological diversity*. Blackwell Publishing, Oxford.

Nekola, J.C. & White, P.S. (1999) The distance decay of similarity in biogeography and ecology. *Journal of Biogeography*, **26**, 867–878.

Novotny, V. & Basset, Y. (2000) Rare species in communities of tropical insect herbivores: pondering the mystery of singletons. *Oikos*, **89**, 564–572.

Novotny, V. & Weiblen, G.D. (2005) From communities to continents: beta diversity of herbivorous insects. *Annales Zoologici Fennici*, **42**, 463–475.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2010) Vegan: community ecology package. R package version 1.17-3. Available at: http://cran.r-project.org (accessed 1 July 2010).

R Development Core Team (2009) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.r-project.org (accessed 1 July 2010).

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. *Kongelige Danske Videnskabernes Selskabs Biologiske Skrifter*, **5**, 1–34.

Tuomisto, H. (2010a) A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography*, **33**, 2–22.

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

Uetz, G.W. (1991) Habitat structure and spider foraging. *Habitat structure: the physical arrangement of objects in space* (ed. by S.S. Bell, E.D. McCoy and H.R. Mushinsky), pp. 325–348. Chapman and Hall, London.

Ulrich, W., Almeida-Neto, M. & Gotelli, N.J. (2009) A consumer's guide to nestedness analysis. *Oikos*, **118**, 3–17.

Urban, M.C., Skelly, D.K., Burchsted, D., Price, W. & Lowry, S. (2006) Stream communities across a rural–urban landscape gradient. *Diversity and Distributions*, **12**, 337–350.

Whittaker, R.H. (1960) Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, **30**, 279–338.

Williams, P.H. (1996) Mapping variations in the strength and breadth of biogeographic transition zones using species turnover. *Proceedings of the Royal Society B: Biological Sciences*, **263**, 579–588.

Williams, P.H., de Klerk, H.M. & Crowe, T.M. (1999) Interpreting biogeographical boundaries among Afrotropical birds: spatial patterns in richness gradients and species replacement. *Journal of Biogeography*, **26**, 459–474.

Wise, D.H. (1993) *Spiders in ecological webs.* Cambridge University Press, New York.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Composition of spider assemblages in costal dunes with natural vegetation and invaded by *Acacia* sp.
Appendix S2 Composition of spider assemblages in costal dunes along a latitudinal gradient.

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