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Partitioning taxon, phylogenetic and functional beta diversity into replacement and richness difference components

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ABSTRACT

Aim To propose a unified framework for quantifying taxon (Tβ), phylogenetic (Pβ) and functional (Fβ) beta diversity via pairwise comparisons of communities, which allows these types of beta diversity to be partitioned into ecologically meaningful additive components.

Location Global, with case studies in Europe and the Azores archipelago.

Methods Using trees as a common representation for taxon, phylogenetic and functional diversity, we partition total beta diversity (β_{total}) into its replacement (turnover, β_{repl}) and richness difference (β_{rich}) components according to which part of a global tree was shared by or unique to communities that were being compared. We demonstrate the application of this framework using artificial and empirical examples (mammals in Europe and epigean arthropods in the Azores).

Results Our empirical examples show that comparing Pβ and Fβ with the most commonly used Tβ revealed previously hidden patterns of beta diversity. More importantly, we demonstrate that partitioning Pβ_{total} and Fβ_{total} into their respective β_{repl} and β_{rich} components facilitates the detection of more complex patterns than using the overall coefficients alone, further elucidating the different forces operating in community assembly.

Main conclusions The methods presented here allow the integration and full comparison of Tβ, Pβ and Fβ. They provide a tool for effectively disentangling the replacement (turnover) and richness difference components of the different biodiversity facets within the same methodological framework.

Keywords

Azores, arthropods, beta diversity metrics, differentiation, dissimilarity, European mammals, functional diversity, phylogenetic diversity, taxonomic diversity, turnover.

INTRODUCTION

Assessing, measuring and interpreting biodiversity in space and time are challenging tasks in ecology, evolution, biogeography and conservation. The notion of taxon diversity (TD) is the most common and is quantified in many different ways based on the number of taxa and, often, on the distribution of abundances. TD treats taxa as being equally distinct from one another and disregards the fact that communities are composed of species with different evolutionary histories (Webb *et al.*, 2002; Graham & Fine, 2008) and a diverse array of ecological functions (Villéger

et al., 2012, 2013). Thus, the last decade has seen a growing interest in alternative representations of biodiversity, including phylogenetic diversity (PD) and functional diversity (FD) (Devictor *et al.*, 2010; Meynard *et al.*, 2011; Stegen & Hurlbert, 2011). Although TD, PD and FD may be correlated, they can reveal different mechanisms associated with the origin and maintenance of biodiversity. Note that although the terms 'phylogenetic diversity' and 'functional diversity' have been used to refer to a specific class of measures, we use them as generic terms for any method for integrating phylogenetic or functional information into diversity measures.

Phylogenetic diversity takes the evolutionary relationships between taxa into account (Faith, 1992) and reflects how much evolutionary history is behind the species in the community. Communities with identical TD may differ widely with respect to their evolutionary past, depending on how far the species have diverged from their nearest common ancestor (Webb *et al.*, 2002; Graham & Fine, 2008). PD has mostly been measured based on phylogenetic trees or cladograms. The available measures encompass either the amount of phylogenetic information conveyed by the community – e.g. the minimum length of tree edges connecting all taxa (Faith, 1992) – or the degree of (un)relatedness of taxa – e.g. the average node distance between them in the phylogenetic tree (Webb *et al.*, 2002; but see Helmus *et al.*, 2007, for alternative measures).

In lieu of precise phylogenetic information on the member taxa of a community, taxonomic diversity (LD, the abbreviation referring to Linnaeus) may be used as a surrogate for PD, and may be calculated in a similar way from an ultrametric tree (i.e. a dissimilarity matrix) representing the Linnaean hierarchy (Ricotta *et al.*, 2012). Consequently, LD uses the hierarchical classification of organisms, whereas TD does not, and it approximates the amount of information provided by PD with variable success depending on how closely the Linnaean system represents the phylogeny as hypothesized by the phylogenetic tree. Thus, 'taxon' and 'taxonomic' diversity are not the same; the first refers to a partition, whereas the second refers to a hierarchy.

Functional diversity quantifies the components of biodiversity that influence how an ecosystem operates or functions (Tilman *et al.*, 2001). Communities with completely different species composition may be characterized by low variation in functional traits, with unrelated species replacing others with similar roles in the network (Villéger *et al.*, 2012, 2013). FD has also been quantified in many different ways, often using approaches that were first developed for PD, such as quadratic entropy (Rao, 1982), dendrogram-based measures (Petchey & Gaston, 2002, 2006) or the functional hyperspace occupied by taxa (Villéger *et al.*, 2013).

Although β-diversity has been most frequently studied at the taxon level (i.e. Tβ), as originally suggested (Whittaker, 1960; Anderson *et al.*, 2011), there is growing demand to understand the phylogenetic and functional components of community variation as well (see Swenson, 2011, and references therein). This inevitably leads to β being defined in terms of the phylogenetic or functional relatedness of member species of a given community. Phylogenetic beta diversity (Pβ) allows one to discriminate phylogenetically basal and terminal changes (branch points occurring early and late in a phylogeny) between communities, a feature that is impossible to reveal using taxon-based analyses (Graham & Fine, 2008). Functional beta diversity (Fβ) intends to discriminate change between communities of taxa with either similar or different functions in the system (see, for example, Ricotta & Burrascano, 2008).

Many β measures proposed to date reduce the calculations to pairwise comparisons of communities. Examples are the two most commonly used Pβ measures: UniFrac (a phylogenetic equivalent of the Jaccard index; Lozupone & Knight, 2005) and PhyloSor (a phylogenetic equivalent of the Sørensen index; Bryant *et al.*, 2008) (see also Rao's quadratic entropy as a common measure for Tβ, Pβ and Fβ; Devictor *et al.*, 2010; but see Chao *et al.*, 2010, for problems using Rao's entropy because of nonlinearity with increasing diversity). These indices are applied to tree representations of communities: a phylogenetic tree is obtained for the member species, and the coefficients are calculated from the matching and mismatching edges of the tree. Each coefficient has different (dis)advantages and interpretations (e.g. Swenson, 2011; Feng *et al.*, 2012); it is difficult to infer process from pattern because the coefficients do not provide information about exact drivers. Therefore, compositional differences driven by true replacement of lineages are not distinguishable from differences that are driven by the loss (or gain) of entire lineages (Leprieur *et al.*, 2012). The same could be said of all Fβ measures, because they do not separate compositional changes due to true replacement of functional traits from differences due to the loss (or gain) of traits (Villéger *et al.*, 2013).

A solution is offered by beta-diversity partitioning, i.e. separating components that originate from different underlying processes (not to be confounded with gamma-diversity partitioning into alpha and beta components; Lande, 1996; Veech *et al.*, 2002; Jost, 2007). Pioneering work in beta diversity partitioning was conducted by Baselga (2010), who suggested partitioning Tβ into turnover and nestedness-resultant dissimilarity fractions, as derived from both the Sørensen and Jaccard indices (Baselga, 2010, 2012). These approaches were adapted to the analysis of Pβ (Leprieur *et al.*, 2012) and Fβ (Villéger *et al.*, 2013), but such methods present several shortcomings (see below; Schmera & Podani, 2011; Almeida-Neto *et al.*, 2012; Carvalho *et al.*, 2012, 2013). We have previously demonstrated how Tβ should be disentangled into algebraically comparable fractions, reflecting the replacement and loss (or gain) of taxa in an ecologically meaningful manner (Schmera & Podani, 2011; Carvalho *et al.*, 2012, 2013). It has been shown that partitioning total Tβ into such components has significantly improved our understanding of community organization in space and time (Baiser *et al.*, 2012; Marini *et al.*, 2013).

Our objective is to extend this taxon-based approach to phylogenetic and functional analyses. This unified framework allows meaningful comparisons of all aspects of beta diversity (Tβ, Pβ and Fβ) and their replacement and richness difference components. We demonstrate its application using theoretical and empirical data sets.

A UNIFIED FRAMEWORK FOR TAXON, PHYLOGENETIC AND FUNCTIONAL BETA DIVERSITY

The proposed framework uses a global tree $G = (V, E)$ that is derived from phylogenetic or functional data for the

members of all the communities of interest. G comprises a set V of nodes or vertices and a set E of lines or edges. The terminal vertices in G correspond to taxa (often species), whereas interior nodes represent either sister-group relationships in cladograms or fusion steps in hierarchical classifications. For each community, we select those edges that connect the terminals (taxa) to the root of the global tree. Hence, for each community j, we obtain a community tree $G_j = (V_j, E_j)$, which is a subtree of the global tree. Note that taxon diversity (TD) can also be visualized using a tree diagram, although it is a very special one: in its global tree, each taxon is linked directly to the root by an edge of unit length (star tree). Thus, tree diagrams provide a common basis for an unequivocal comparison of TD, PD (or its surrogate, LD) and FD. Using this general framework, α-diversity (Tα, Pα or Fα) for a given community j is given by:

$$\alpha_j = \sum_{e_x \in E_j} l_x,$$

where l_x represents the length (l) of edge e_x in G_j. Thus, α_j is the length of tree G_j.

Total dissimilarity, understood here as the total pairwise β of communities j and k, corresponds to the sum of the lengths of edges that are unique to each community tree:

$$\text{total dissimilarity}_{jk} = \sum_{e_x \in E_j} l_x + \sum_{e_x \in E_k} l_x - 2 \sum_{e_x \in E_j \cap E_k} l_x.$$

This equation was implicitly or explicitly part of previous methods describing total phylogenetic dissimilarity (UniFrac, Lozupone & Knight, 2005; PhyloSor, Bryant et al., 2008). Our basic idea is that total dissimilarity can be partitioned additively into two fractions – replacement and richness difference. The first one corresponds to the substitution of edges exclusive to community j by other edges with the same total length that are exclusive to k. Algebraically, the replacement fraction of the total dissimilarity is given by twice the minimum of the sum of the lengths of edges that are unique to each community:

$$\text{replacement}_{jk} = 2 \min \left\{ \sum_{e_x \in E_j \cup E_k} l_x - \sum_{e_x \in E_j} l_x, \sum_{e_x \in E_j \cup E_k} l_x - \sum_{e_x \in E_k} l_x \right\}.$$

The remaining dissimilarity fraction corresponds to difference in α-diversity or richness, and is quantified by the absolute difference between the lengths of G_j and G_k:

$$\text{richness difference}_{jk} = \left| \sum_{e_x \in E_j} l_x - \sum_{e_x \in E_k} l_x \right| = \left| \alpha_j - \alpha_k \right|.$$

In fact, the total dissimilarity measure is the algebraic sum of the replacement and richness difference measures. Finally, all these quantities must be scaled in relation to a common denominator. This should be the sum of the lengths of edges

that are part of either community j or k, including shared edges, i.e. gamma diversity in a pairwise comparison:

$$\gamma_{jk} = \sum_{e_x \in E_j \cup E_k} l_x.$$

From a different, complementary perspective, pairwise beta diversity has traditionally been measured by comparing the matching/mismatching components of a 2×2 contingency table (Nipperess et al., 2010; Legendre & Legendre, 2012). These components are the number of features (a) common to both communities, (b) present in the first community only, (c) present in the second community only, and (d) absent from both communities but present elsewhere in the region of interest. Such features are usually species. For tree representations, the features of interest are not species but edges, which may have different lengths and be shared by different species which may be present in different communities (Fig. 1). Following Nipperess et al. (2010), the matching component a is the sum of the lengths of the edges pertaining to taxa shared by both communities j and k:

$$a = \sum_{e_x \in E_j \cap E_k} l_x.$$
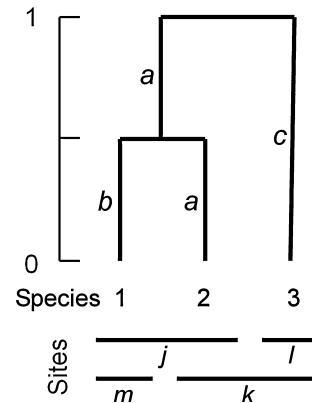
Figure 1 Theoretical example of a phylogenetic or functional tree, with three species and four communities. The matching (a) and mismatching (b, c) components between two communities (j, k) are also shown. Comparison of j and k is an example of species replacement without richness difference in a taxon-based analysis because each has two species. Because k has a longer exclusive edge adjacent to species 3 than j has to species 1, part of total phylogenetic beta diversity (Pβ_{total}) or total functional beta diversity (Fβ_{total}) is due to richness difference (Table 1). Communities j and l have no species or edges in common. However, edges connecting the species of j to the root are longer than the single edge in l (1.5 vs. 1 unit), and this is reflected in the richness difference fraction. Communities j and m or k and l illustrate cases of pure loss of species and associated edges with no replacement. Communities k and m have no species in common, but share one edge; hence, Pβ_{total} or Fβ_{total} is lower than 1. Communities l and m share neither species nor edges, and both have the same alpha diversity, leading to maximum replacement and no richness difference.

The mismatching component b is the sum of the lengths of the edges pertaining to taxa present in j but not in k:

$$b = \sum_{e_x \in E_j} l_x - \sum_{e_x \in E_j \cap E_k} l_x = \alpha_j - a.$$

Analogously, the mismatching component c is the sum of the lengths of the edges pertaining to taxa present in k but not in j:

$$c = \sum_{e_x \in E_k} l_x - \sum_{e_x \in E_j \cap E_k} l_x = \alpha_k - a.$$

Therefore, $\gamma_{jk} = a + b + c$. The parameter d is not used in beta diversity measures, because double zeros are usually considered uninformative (Legendre & Legendre, 2012). Based on these matching/mismatching components, it is now possible to formally link our new measures to previous approaches for partitioning pairwise $T\beta$ (Podani & Schmera, 2011; Carvalho *et al.*, 2012). β_{total} is therefore

$$\beta_{\text{total}} = \frac{\sum_{e_x \in E_j} l_x + \sum_{e_x \in E_k} l_x - 2 \sum_{e_x \in E_j \cap E_k} l_x}{\sum_{e_x \in E_j \cup E_k} l_x} = \frac{b + c}{a + b + c}.$$

When applied to TD, β_{total} is equivalent to pairwise beta diversity as expressed by the Jaccard index of dissimilarity. For quantitative data, such as edge lengths, Jaccard dissimilarity is in fact a generalization to the Marczewski–Steinhaus coefficient of dissimilarity that is often used in multivariate analysis (Podani *et al.*, 2013). This measure is better known as UniFrac (Lozupone & Knight, 2005) in PD studies.

Relativized beta due to replacement or turnover (β_{repl}) is as follows:

$$\beta_{\text{repl}} = \frac{2 \min \left\{ \sum_{e_x \in E_j \cup E_k} l_x - \sum_{e_x \in E_j} l_x, \sum_{e_x \in E_j \cup E_k} l_x - \sum_{e_x \in E_k} l_x \right\}}{\sum_{e_x \in E_j \cup E_k} l_x}$$

$$= \frac{2 \min\{b, c\}}{a + b + c}.$$

When applied to TD, β_{repl} is equivalent to beta diversity derived from the Williams β_{-3} measure, as modified by Cardoso *et al.* (2009).

Finally, relativized pairwise beta due to richness difference among communities (β_{rich}) is as follows:

$$\beta_{\text{rich}} = \frac{\left| \sum_{e_x \in E_j} l_x - \sum_{e_x \in E_k} l_x \right|}{\sum_{e_x \in E_j \cup E_k} l_x} = \frac{|b - c|}{a + b + c}.$$

When applied to TD, β_{rich} is equivalent to the beta diversity derived from species richness difference, as defined by Podani & Schmera (2011) and Carvalho *et al.* (2012). Note

that a similar formula, derived from the Sørensen index, was proposed by Lennon *et al.* (2001). Because the denominator is identical in the above three equations, we may derive the following:

$$\beta_{\text{total}} = \beta_{\text{repl}} + \beta_{\text{rich}}.$$

THEORETICAL CASES

A small theoretical dataset

To better understand the application of the novel framework, we first use a theoretical representation of either a phylogenetic or a functional global tree for a given sampled universe (Fig. 1, Table 1). All measures behave in an intuitive way, correctly reflecting the different proportions of replacement and richness difference.

A large theoretical dataset

The behaviour of the new measures was also tested for scenarios in which edges with increasing or decreasing length in a fully chained global tree were gradually lost/gained or replaced (Fig. 2). We tested both pure richness difference (the loss of species leading to loss of edges) and pure species replacement (keeping constant the number of species). In each modelled situation, comparisons were made between a single reference community (line on top of Fig. 2) and each subsequent community (all others below).

Pure richness difference

In the first two cases (Loss 1 and Loss 2), $T\beta_{\text{total}}$ and $T\beta_{\text{rich}}$ increase linearly, whereas $P\beta_{\text{total}}$ or $F\beta_{\text{total}}$ and $P\beta_{\text{rich}}$ or $F\beta_{\text{rich}}$ exhibit a curvilinear increase with increasing loss of species, depending on the direction in which the edges were lost (Fig. 3). For Loss 1, because the short edges of the tree are removed first, $P\beta_{\text{total}}$ or $F\beta_{\text{total}}$ and $P\beta_{\text{rich}}$ or $F\beta_{\text{rich}}$ increase slowly, with larger increases when the longer edges are lost. In Loss 2, because the longer edges are lost first, $P\beta_{\text{total}}$ (or $F\beta_{\text{total}}$) and $P\beta_{\text{rich}}$ (or $F\beta_{\text{rich}}$) increase rapidly but then level off when the removed edges decrease in length. β_{repl} is zero in all cases.

Table 1 Matching/mismatching components (a, b, c) and beta diversity values of all possible pairwise comparisons of communities in the theoretical example shown in Fig. 1.

	Communities					
	j, k	j, l	j, m	k, l	k, m	l, m
a	1	0	1	1	0.5	0
b	0.5	1.5	0.5	1	1.5	1
c	1	1	0	0	0.5	1
β_{total}	0.6	1	0.333	0.5	0.8	1
β_{repl}	0.4	0.8	0	0	0.4	1
β_{rich}	0.2	0.2	0.333	0.5	0.4	0
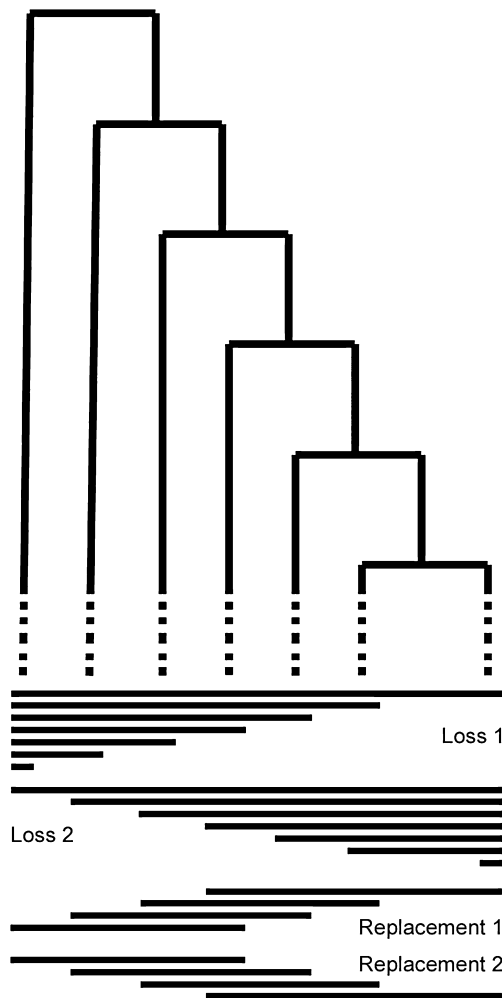
Figure 2 Theoretical example of a phylogenetic or functional tree with 100 species (to save space, only a part of the tree is shown; the tree continues to the right and down). Four examples with 100 communities each were created (thick lines show only a few of those). In relation to the first reference community (top line in each model), the first two examples show a pure loss of species, either with the short or the long edges removed first. The third and fourth scenarios represent a pure replacement of species in which species are replaced either with short or long edges removed first.

Pure replacement

The second two cases (Replacement 1 and Replacement 2) were constructed such that the number of replaced species increases monotonically and gamma diversity also increases in the same direction. As a consequence, the proportion of replaced species increases steeply at the beginning, when gamma is low (Fig. 3). This is reflected in both $T\beta_{total}$ and $T\beta_{repl}$; $T\beta_{rich}$ remains at zero. When applied to the phylogenetic or functional tree, the progressive species replacements lead to radically different results. In Replacement 1, the tree of the reference community includes the shorter edges; at first, these edges are mostly replaced, and $P\beta_{rich}$ (or $F\beta_{rich}$) increases rapidly as the newly added edges represent a large proportion

of gamma. $P\beta_{rich}$ (or $F\beta_{rich}$) later stabilizes, as the added edges represent a smaller proportion from the increasing gamma diversity. $P\beta_{repl}$ (or $F\beta_{repl}$) increases monotonically and becomes similar to $P\beta_{rich}$ (or $F\beta_{rich}$) when replacement is complete; $P\beta_{total}$ (or $F\beta_{total}$) follows the same trend as $T\beta_{total}$. In Replacement 2, the tree of the reference community includes only long edges; these are replaced first, and $P\beta_{repl}$ (or $F\beta_{repl}$) increases rapidly at the beginning. $P\beta_{repl}$ (or $F\beta_{repl}$) later stabilizes, as shorter edges are replaced. $P\beta_{rich}$ (or $F\beta_{rich}$) increases monotonically and becomes similar to $P\beta_{repl}$ (or $F\beta_{repl}$); $P\beta_{total}$ (or $F\beta_{total}$) follows the same trend as $T\beta_{total}$.

Benchmark testing

All diversity measures are capable of producing Type I and II errors when tested for statistical significance. Measures prone to Type I errors will often identify communities as deviating from randomness even when this is not the case. Measures prone to Type II errors will often not identify true deviations from randomness. To assess the robustness of the new measures to Type I and Type II errors, we performed a 'noise test' (Gotelli *et al.*, 1997; Gotelli, 2000). We used data matrices with two assemblages and 100 species. When testing the detection of richness difference, the first assemblage contained 100 species, and the second contained zero species. When testing the detection of replacement, both assemblages contained 50 species, none of which were shared. Starting from these data and using both a star phylogeny (to test the indices when applied to taxon diversity – TD) and the dendrogram described in Fig. 2 (to test the indices when applied to phylogenetic or functional diversity – PD or FD), the species incidences were progressively interchanged, with one random change between presence and absence from each assemblage at each step with replacement (so that some species incidences may change multiple times, whereas others never change). Changes were independent for each assemblage in the pair. One hundred noise steps (added random variation) were performed, and the process was repeated 1000 times to obtain average values. In order to obtain a *P*-value for each beta measure at each noise step, the averaged observed beta values were compared to a distribution of random beta values obtained from 1000 random assemblage pairs, where each species had a 50% chance of being present in each assemblage. The proportion of β values at each noise step that could potentially be regarded as resulting from random communities was calculated as the *P*-value of this test (probability of Type I error if the null hypothesis of a random process is rejected). Ideally, a measure would remain significantly different from random with low levels of noise and would not differ from random with high levels of noise, with a sharp turning point at intermediate levels (Gotelli, 2000). The measure is prone to Type I errors if it indicates the existence of a pattern at high levels of noise and to Type II errors if it requires little noise to obscure the pattern.

The pure loss process is undetected after approximately 20 interchanges in the case of β_{total} and after approximately 50
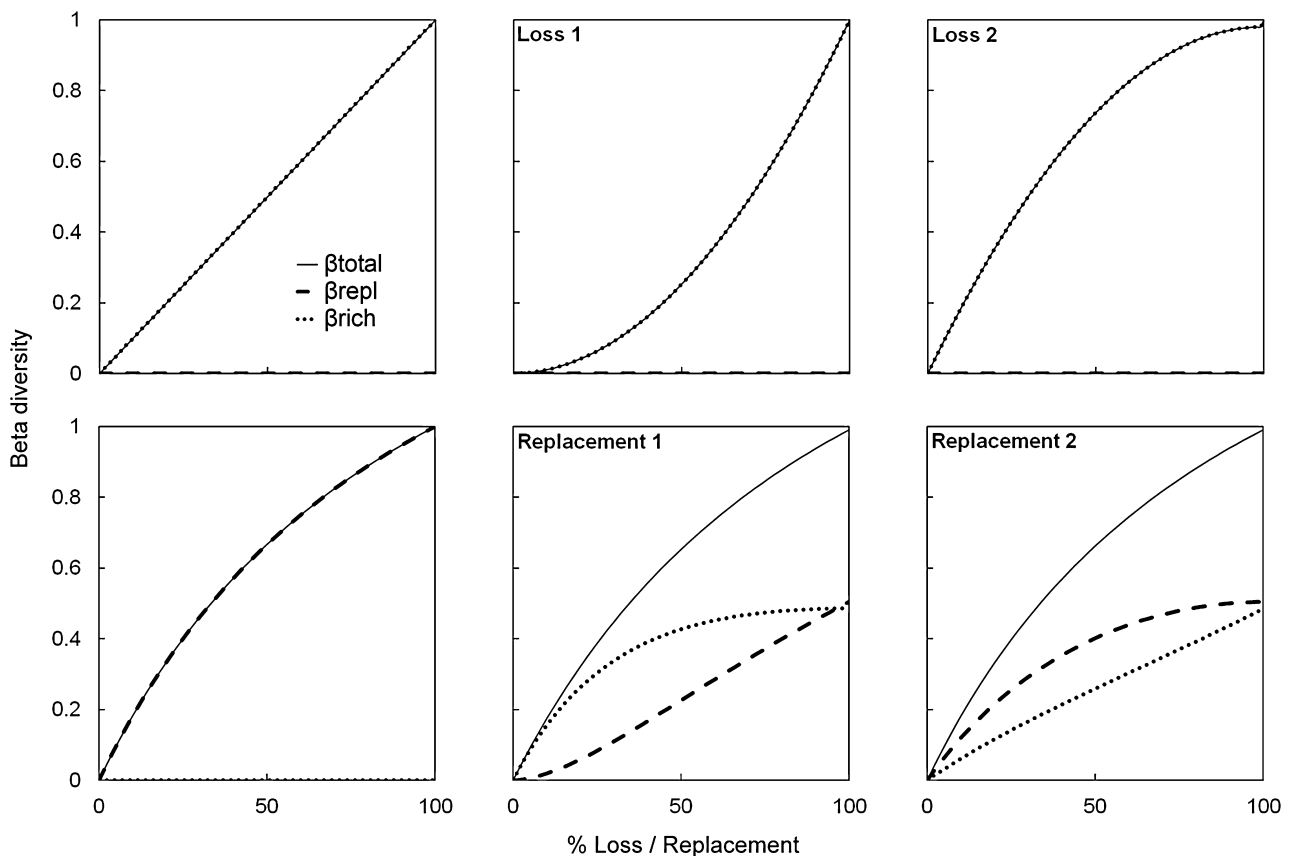
Figure 3 Results of model studies shown in Fig. 2. Top row, loss models; bottom row, replacement models. The left panels show changes in taxon beta diversity (Tβ); the middle and right panels show changes in phylogenetic beta diversity (Pβ) and functional beta diversity (Fβ), as measured with the trees and scenarios in Fig. 2. β_{total}, total beta diversity; β_{repl}, beta diversity due to replacement; β_{rich}, beta diversity due to richness difference.

to 70 interchanges in the case of β_{repl} and β_{rich} for both taxon and phylogenetic/functional diversity (Fig. 4). As random assemblage pairs have relatively similar species richness and high replacement, and because the starting point is opposite to this, the measures are very robust to high random variation in the datasets, yet do not differ from randomness when they are in fact mostly random.

The pure replacement process for taxon diversity is undetected after approximately 20 interchanges in the case of β_{total} and β_{repl}. Because random assemblage pairs present similar richness, observed β_{rich} (starting with 0) never differs from random, as expected for this particular test. For phylogenetic/functional diversity, and given the topology of the tree, β_{repl} never differs from the random expectation. β_{total} and β_{rich} lose significance after approximately 20 to 30 interchanges (Fig. 4). All measures reflect randomness when assemblages are mostly random.

EMPIRICAL CASES

We use two empirical examples to demonstrate that, in many practical cases, (1) measuring Pβ and Fβ may provide insights that simple Tβ masks, and (2) it is fundamental to

distinguish between the β_{repl} and β_{rich} components of β_{total} if the observed patterns are to be fully understood and their causes are to be correctly established. Additionally, a small dataset is used to compare the new framework with previous approaches (Baselga, 2010, 2012; Leprieur *et al.*, 2012; Villéger *et al.*, 2013; see Appendix S1 in Supporting Information). All the statistical analyses were implemented within the R programming environment (R Development Core Team, 2010).

Phylogenetic diversity on a large spatial scale

The Atlas of European Mammals (Mitchell-Jones *et al.*, 1999) provides the distribution of the 160 native mammals in Europe in a 50 km × 50 km resolution. We built the phylogenetic tree for these species by extracting phylogenetic relationships from the world-wide mammal supertree provided by Bininda-Emonds *et al.* (2007). We first downloaded the tree from http://www.evoio.org/wiki/File:Bininda-emonds_2007_mammals.nex (downloaded 1 March 2013). We then pruned the tree by keeping only tips that matched the species list of European mammals. Tree manipulations were achieved using the APE R package (Paradis *et al.*, 2004). We
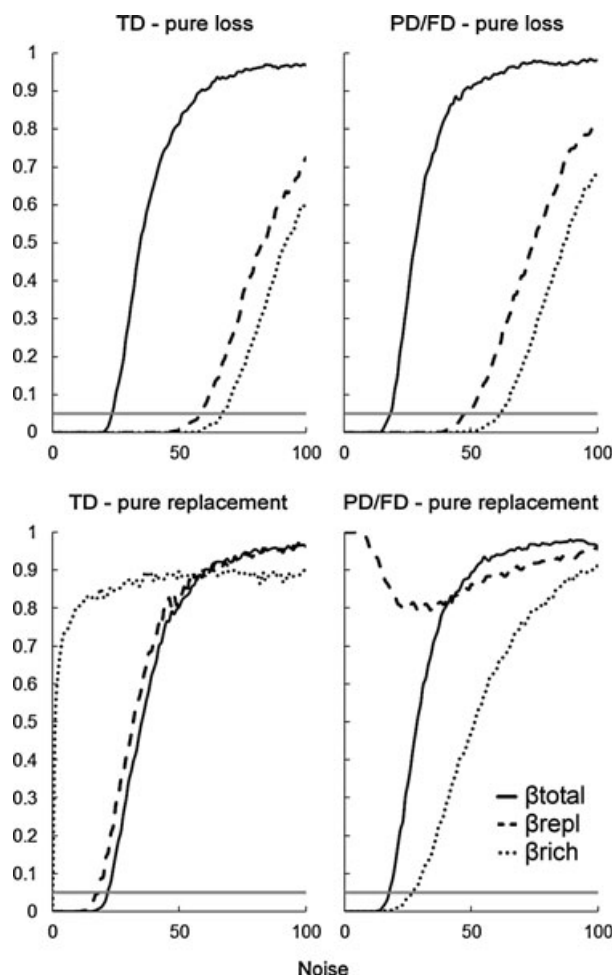
Figure 4 Benchmark testing of the new measures (TD, taxon diversity; PD/FD, phylogenetic and functional diversity). Starting with datasets with maximum richness difference (upper panels) or replacement (lower panels), the presence of species in the assemblages was progressively randomized (the *x*-axis represents noise added). The *y*-axis represents the mean *P*-value over the 1000 iterations of each benchmark testing scenario, i.e. the probability of error if the null hypothesis of a random process is rejected. In all cases, horizontal grey lines represent $P = 0.05$. β_{total}, total beta diversity; β_{repl}, beta diversity due to replacement; β_{rich}, beta diversity due to richness difference.

then calculated matrices among all cells using the taxon and phylogenetic beta diversity measures as entries. We performed hierarchical agglomerative clustering of grid cells for each matrix separately, using the Ward method. A penalty function (Kelley–Gardner–Sutcliffe Kelley *et al.*, 1996) was used to identify distinct clusters of cells. This method's minimum value corresponds to the optimal number of clusters, which is intended to represent biogeographical regions. Additionally, we calculated Tα and Pα for each cell.

Tα and Pα follow similar trends, with higher values at intermediate latitudes (Fig. 5). The use of Tβ_{total} and Pβ_{total} each identifies five clusters. Although the taxon data separate western and eastern Mediterranean areas, phylogenetic data result in a single Mediterranean cluster. Areas of low Tα and

Pα are also clustered together (e.g. parts of Scandinavia with the Mediterranean), reflecting the influence of α in β_{total}. The analysis of Tβ_{repl} and Pβ_{repl} leads again to five clusters, but the pattern is clearer, with northern and central European regions and then a roughly western, central and eastern division of the Mediterranean, each extending further north than the true Mediterranean region. Taxon and phylogenetic data differ, with southern France, Greece and Norway belonging to different clusters. Tβ_{rich} and Pβ_{rich} both follow the trend of α-diversity as expected, with the identification of four clusters.

Functional diversity on a small spatial scale

The North Atlantic Azorean archipelago, with nine islands, presents a mosaic of land uses that replaced the once almost homogeneous cover of laurel forest (Cardoso *et al.*, 2013). A total of 72 sites arranged along a continuous gradient of disturbance according to land use and the surrounding habitat matrix in Terceira Island were sampled for epigean arthropods. The collected species were classified as endemic, native non-endemic or exotic (Cardoso *et al.*, 2013). Functional characteristics related to resource use were collated for all the arthropod species and a functional tree was built (see Appendix S2). Based on the distribution of 32 endemic, 76 native non-endemic and 129 exotic species and their respective functional relationships in the global functional dendrogram, we then calculated taxon and functional beta-diversity matrices for all communities. We performed regressions with disturbance value differences between all possible pairs of sites as the explanatory variables and all beta diversity measures as response variables, and then tested significance with Mantel tests.

In all cases, Tβ_{total} and Fβ_{total} significantly increase with increasing differences in habitat disturbance (Fig. 6, Appendix S2), but for endemics the patterns are caused by increasing Tβ_{rich} and Fβ_{rich}, reflecting a loss (or gain) of endemic species richness and their functions with changing disturbance. On the contrary, for native non-endemic species, the patterns follow Tβ_{repl} and Fβ_{repl}, reflecting a substitution of some species by others performing different functions. The patterns for exotic species are different depending on the use of taxon or functional data. Whereas Tβ_{rich} causes the pattern of taxon beta, Fβ_{repl} causes the functional pattern. This difference reflects a change of exotic species richness along the gradient of disturbance but mostly a replacement of functions along the same gradient.

DISCUSSION

Using a range of both theoretical and empirical examples, we confirm that taxon data – i.e. species identities alone – do not allow the recovery of patterns and processes that require information on how species are phylogenetically related and/ or how they exploit and share resources. The unified framework used here combines taxon, phylogenetic and functional
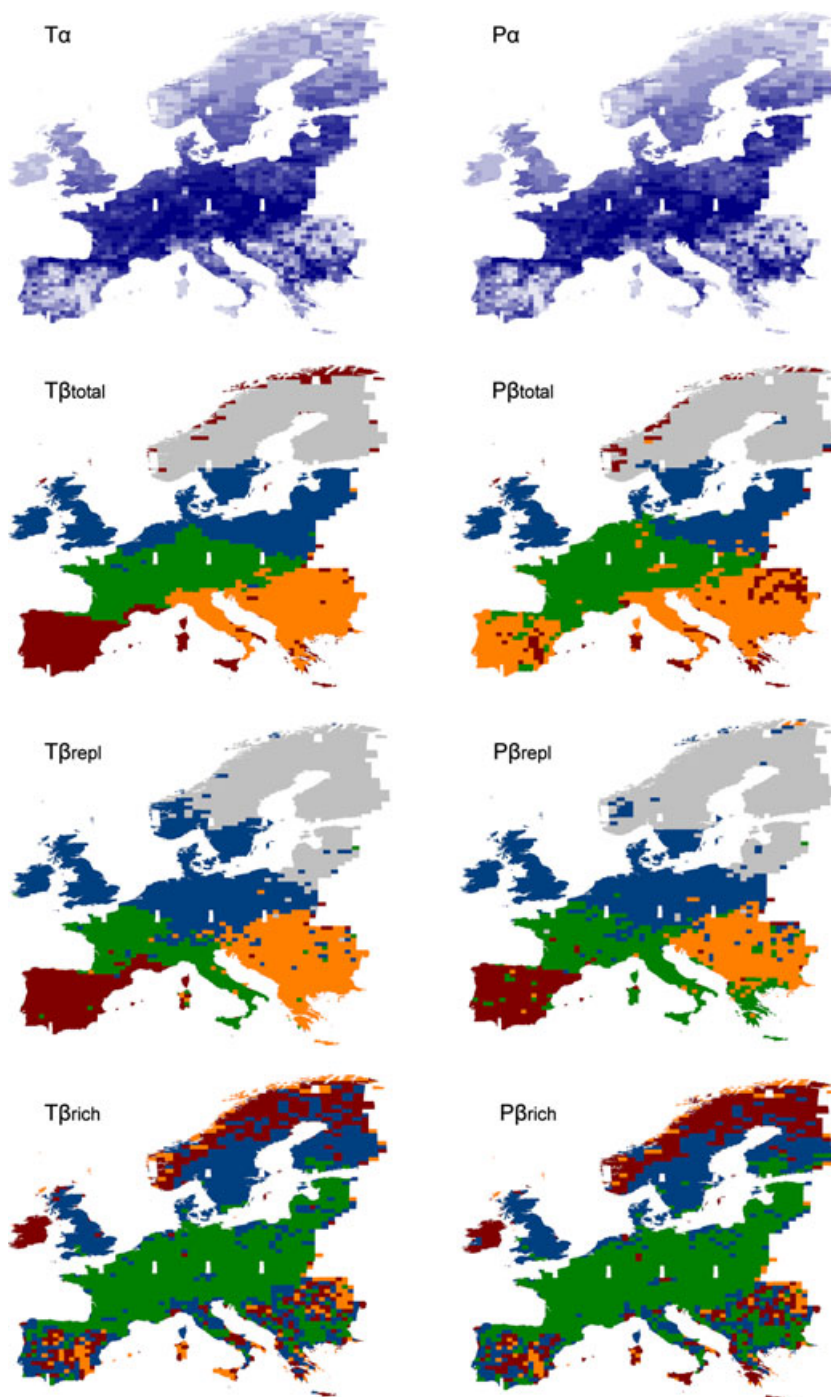
Figure 5 Geographical distribution of clusters derived from taxon beta diversity (Tβ) and phylogenetic beta diversity (Pβ) data of European mammals. Different colours/shades represent different clusters. Maps of α-diversity are shown for comparison, with darker shades representing higher values. Owing to coordinate mismatch, interspersed blank areas have no data. β_{total}, total beta diversity; β_{repl}, beta diversity due to replacement; β_{rich}, beta diversity due to richness difference.

diversity into a single tree-based approach, offering meaningful comparisons between these facets of biological diversity using the same set of community data.

We demonstrate that 'catch-all' beta diversity measures, such as UniFrac or PhyloSor, do not allow differences driven by the replacement of lineages or functional traits to be distinguished from those driven by the loss (or gain) of entire lineages or traits. Our approach to diversity partitioning differs from the methods suggested by Baselga (2010, 2012), Leprieur *et al.* (2012) and Villéger *et al.* (2013) in that pairwise dissimilarities between communities are explicitly

separated into a component from replacement and another corresponding to richness difference. The previous approaches consistently overestimate the part of beta diversity that derives from true replacement and underestimate the part that derives from richness difference, as previously shown for TD (see also Appendix S1); further advantages are detailed elsewhere (Schmera & Podani, 2011; Carvalho *et al.*, 2012, 2013).

The different measures also do not appear to be prone to either Type I or Type II errors. They are able to detect patterns with moderate to high amounts of random variation in
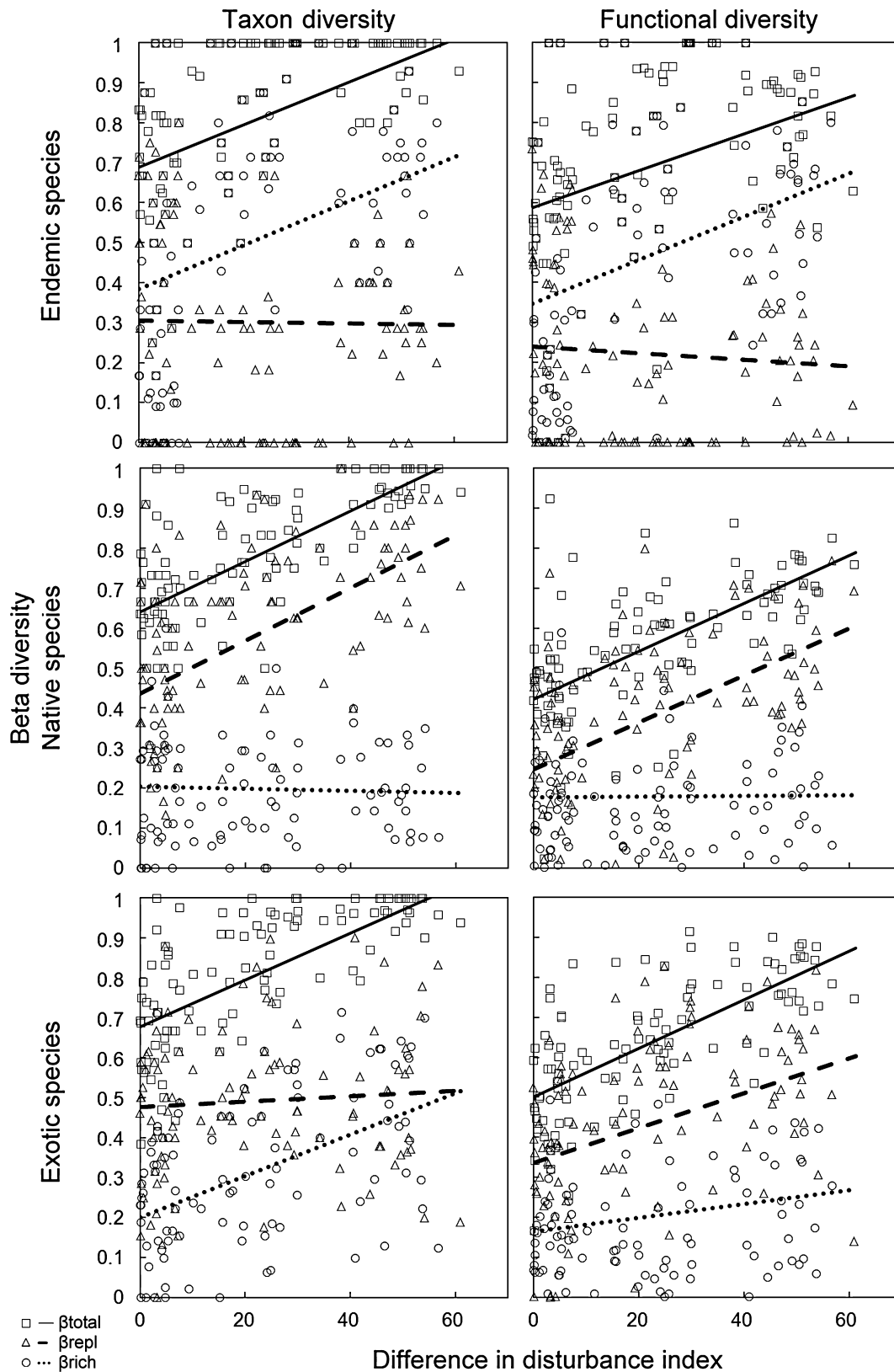
Figure 6 Linear regressions of differences in disturbance index and beta diversity among all possible pairs of 72 sites in Terceira Island (Azores) that were sampled for arthropods. Only 100 dots per regression are shown for clarity. β_{total}, total beta diversity; β_{repl}, beta diversity due to replacement; β_{rich}, beta diversity due to richness difference. See Appendix S2 for the slope, r^2 and significance values.

the data (have good statistical power) and the measures do not differ from random values when communities are indeed mostly random (low Type I error rate). In the pure replacement scenario, β_{rich} of taxon diversity and β_{repl} for phylogenetic and functional diversity were never significant (different from random values) simply because the testing scenario did not alter richness or the phylogeny or functional characteristics of the species.

Phylogenetic diversity of European mammals

Depending on the diversity measure used, our clusters either do or do not match those previously obtained by Heikinheimo *et al.* (2007). During the analysis of total beta diversity, one or two large southern European clusters appear, with south-western and south-eastern Europe being differentiated when no phylogenetic information is taken into account. The analysis of β_{repl} alone presents a different perspective from this and from Heikinheimo *et al.* (2007), with southern Europe being divided into three areas, roughly corresponding to the Mediterranean peninsulas. It appears that richness differences were confounding the species-level turnover between regions of southern Europe. These areas acted as glacial refugia and are often thought to harbour greatly different faunas, although they are currently depauperate compared with central Europe. However, a similar level and pattern of provinciality have been characteristic of the European mammal fauna for millions of years (Maridet *et al.*, 2007; Costeur & Legendre, 2008). In the fossil data, the degree to which the peninsulas are separate is strongly dependent on the taxonomic level analysed: genus-level analyses yield a much weaker pattern of endemism than species-level analyses. The high replacement of species and lineages between the peninsulas observed in our analysis may similarly be due to the presence of local species-level endemics. This indicates that, although the Iberian Peninsula differs in terms of species composition, this region shares a common phylogenetic history with other Mediterranean areas.

Richness differences should, in principle, be higher in areas with stronger environmental gradients, when extremes of cold or drought are reached. Such extremes could cause the fine-scale variation of β_{rich} within the Iberian and Balkan peninsulas, with a marked loss of species in particularly arid ecosystems (Casanovas-Vilar & Agustí, 2007). Additionally, the fossil record reveals a pattern of basin-level endemism in the Iberian Peninsula, especially for small non-volant mammals (Agustí, 1990).

The reasons for separation of the Mediterranean peninsulas from the continental clusters differ from one another. For Iberia, the main factor is undoubtedly geographical isolation with consequent endemism (van der Meulen *et al.*, 2011). For Italy, the situation is somewhat similar today, although its geological history is much more complicated (Rook *et al.*, 2006). For the Balkans, the background is different in that this area forms the westernmost extension of many Asian biotas, which, when Asia is excluded from the analysis, causes the region to appear highly 'endemic' (Maridet *et al.*, 2007; Costeur & Legendre, 2008).

Functional diversity of Azorean arthropods

The similar increase in $T\beta_{total}$ and $F\beta_{total}$ with increasing habitat disturbance differences for all species groups reveals the presence of species adapted to each extreme of the gradient and the respective functional change. However, partitioning $T\beta_{total}$ and $F\beta_{total}$ into their respective β_{repl} and β_{rich} components reveals that the increases of $T\beta_{total}$ and $F\beta_{total}$ were not driven by the same processes for the different communities. For endemics, $T\beta_{total}$ and $F\beta_{total}$ are simply an outcome of $T\beta_{rich}$ and $F\beta_{rich}$, reflecting the decline of both species and the range of functions they perform along the disturbance gradient. Endemic species are expected to be more sensitive to habitat disturbance, and only a few of them are able to sustain populations outside native forests (Cardoso *et al.*, 2013). The relative stability of $T\beta_{repl}$ and $F\beta_{repl}$ along the gradient indicates that increasing disturbance differences does not increase true taxon and functional turnover between communities. That is, species and functions are replaced to the same degree when comparing similar or very different communities. This last point may reflect the fact that endemics often have very restricted distributions and that even among pristine habitats, the species performing similar functions are replaced. This replacement among seemingly similar habitats is as strong as the replacement of species and traits from pristine to highly disturbed habitats, as only a few endemics are present in the latter. By contrast, $T\beta_{total}$ and $F\beta_{total}$ of native non-endemic species are mainly driven by $T\beta_{repl}$ and $F\beta_{repl}$. This indicates that native species richness is less affected by disturbance intensification and that the replacement of species is coupled with a corresponding replacement of functions. Native non-endemic species communities in highly disturbed habitats are taxonomically and functionally distinct from those occurring in little-disturbed habitats, but both hold similar species richness and a similar range of functions. Contrary to endemic and native non-endemic species, the increase of $T\beta_{total}$ and $F\beta_{total}$ differences with increasing disturbance differences for exotic species is not explained by the same processes. The pattern of $T\beta_{total}$ is mainly driven by $T\beta_{rich}$, reflecting the gain of exotic species when disturbance increases (Cardoso *et al.*, 2013). $T\beta_{repl}$ is constant but greater than zero along the gradient, also revealing an important contribution of the turnover of species to total differentiation, although it tends to retain importance along the gradient. Opposite to this pattern, $F\beta_{repl}$ – reflecting the replacement of functions along the gradient – mostly causes the pattern in $F\beta_{total}$. These findings indicate that less exotic species occur in habitats with low disturbance compared to highly disturbed habitats, but this increase in the number of species is mostly reflected by a replacement of functional traits. With increasing disturbance, many more exotic species encompass only a slightly larger range of traits, even if such traits are completely different along the gradient.

Future perspectives

Comparing TD, PD and FD requires a common framework. Using the methodology proposed here, these three 'dimensions' are fully comparable, because identical measures are applied to all of them. Although we have used trees as a means to guarantee direct comparability of the different dimensions, this framework can be easily adapted to other representations. For example, it is common for functional diversity to be represented in a multidimensional volume, in which case beta diversity and the matching/mismatching components are quantified according to the degree of overlap between the volumes that are occupied by the different communities (Villéger *et al.*, 2013). Additionally, as presented here, the methods consider species presence/absence only, but extension to abundances is possible using a weighting scheme (Cadotte *et al.*, 2010).

Our two empirical examples confirm that comparing Pβ and Fβ with the most commonly used Tβ reveals previously hidden patterns of beta diversity. For instance, a predominant increase in Pβ_{repl} or Fβ_{repl} along a gradient without an equivalent increase in Tβ_{repl} may reflect historical factors that cause entire lineages to be represented in part of the studied area only, either because they are replaced by completely different lineages elsewhere or because environmental factors force the occurrence of different traits in different communities. By contrast, a predominant increase of Pβ_{rich} may reflect dispersal limitation for certain lineages. For example, the inability of some high-level taxa to reach isolated islands is known, causing the disharmony of many oceanic islands (Whittaker & Fernández-Palacios, 2007), probably causing higher Pβ_{rich} than expected by the corresponding Tβ_{rich} values. It may also reflect environmental filtering, which dictates that only species with given traits are able to occupy certain habitats. For example, caves are occupied by taxa that have pre-adaptations to the particular biotic and abiotic conditions that exist in the subterranean realm (Culver & Pipan, 2009), probably causing higher Fβ_{rich} than expected from the corresponding Tβ_{rich} values.

We also demonstrate that partitioning Pβ_{total} and Fβ_{total} into β_{repl} and β_{rich} components reveals more complex patterns than using the overall coefficients alone, further elucidating the different forces operating in community assembly. For instance, if a phylogenetic pattern is dominated by β_{repl}, there is a strong replacement of lineages from community to community without a notable difference in the amount of phylogenetic information encompassed by the different communities. This may occur in islands with similar areas and ages within the same archipelago, each with its own unique radiations. On the contrary, a phylogenetic pattern dominated by β_{rich} may occur in islands with very different areas and/or ages, in which smaller or younger islands present subsets of the species present in larger or older islands, as limited area, time or niche pre-emption may prevent an extensive radiation of lineages (Silvertown *et al.*, 2005). A functional pattern dominated by β_{repl} may occur in habitats that require very different traits but with similar richness. For example, we refer to two different types of forests comprising different tree species but with similar richness of niches for herbivores. By contrast, a functional pattern that is dominated by β_{rich} may reflect environmental filtering that favours certain traits over others along a gradient (Kluge & Kessler, 2011).

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SUPPORTING INFORMATION

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

Appendix S1 Phylogenetic and functional analysis of Christmas Island rats.
Appendix S2 Additional information on the Azorean arthropods analyses.

BIOSKETCH

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