

Comparing methods to separate components of beta diversity

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Summary

1. Two alternative frameworks have been proposed to partition compositional dissimilarity into replacement and nestedness-resultant component or into replacement and richness-difference components. These are, respectively, the BAS (Baselga 2010, *Global Ecology and Biogeography*, **19**, 134–143) and POD (Podani & Schmera 2011, *Oikos*, **120**, 1625–1638) frameworks.

2. We conduct a systematic comparison of parallel components in alternative approaches. We test whether the replacement components derived from the BAS and POD frameworks are independent of richness difference. We also evaluate whether previously reported tests of monotonicity between indices and ecological processes are informative to assess the performance of indices. Finally, we illustrate the consequences of differences between the BAS and POD frameworks using the North American freshwater fish fauna as an empirical example.

3. In the BAS framework, the nestedness-resultant component (β_{jne} or β_{sne}) accounts only for richness differences derived from nested patterns while, in the POD framework, richness-difference dissimilarity (β_{rich} or $\beta_{rich,s}$) accounts for all kind of richness differences. Likewise, the replacement components of both alternative methods account for different concepts. Only the replacement component of the BAS framework (β_{jtu} or β_{sim}) is independent of richness difference, while the parallel component in the POD framework (β_{-3} or $\beta_{-3,s}$) is not (i.e. it is mathematically constrained by richness difference).

4. Therefore, only the BAS framework allows separating (i) the variation in species composition derived from species replacement which is independent of richness difference (i.e. not mathematically constrained by it) and (ii) the variation in species composition derived from nested patterns.

Key-words: beta diversity, community composition, dissimilarity coefficients, nestedness, replacement, richness difference, turnover

Introduction

Strict sense beta diversity (Whittaker 1960; Jost 2007) is defined as the ratio between gamma (regional) and alpha (local) diversities. This quantity properly quantifies the difference among biological communities because alpha and gamma diversities are different if (and only if) the biological communities within the region are different. Therefore, dissimilarity indices that are monotonic transformations of strict sense beta diversity (i.e. Sørensen and Jaccard indices, see Chao, Chiu & Hsieh 2012) are appropriate measures of differences among biological communities. However, the meaning of ‘difference’ applied to biological communities is not unidimensional, as communities can differ in species composition (i.e. some species are replaced by others), species richness (i.e. one community has more species than the other) or both. This duality of difference between biological communities has been known since long ago (Simpson 1943; Harrison, Ross & Lawton 1992;

Williams 1996; Lennon *et al.* 2001), and a multitude of indices have been implemented to emphasize one aspect of dissimilarity, the other, or both together (Koleff, Gaston & Lennon 2003).

More recently, it has been proposed that total dissimilarity (i.e. a monotonic transformation of strict sense beta diversity) can be partitioned into two additive components (Baselga 2010b) accounting for (i) the dissimilarity associated with the replacement of some species by others between assemblages (i.e. spatial turnover sensu Williams 1996; Gaston & Blackburn 2000) and (ii) the dissimilarity associated with species losses in which an assemblage is a strict subset of another (i.e. nestedness-resultant dissimilarity). Subsequently, Podani & Schmera (2011) and Carvalho, Cardoso & Gomes (2012) introduced an alternative method to separate overall dissimilarity into two additive components accounting for (i) species replacement and (ii) richness differences associated with species losses and gains irrespective of nestedness. Posterior contributions have shown that either methodological approach can be applied to both Sørensen and Jaccard indices, to their abundance-based versions (Baselga 2012, 2013; Podani, Ricotta &

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Schmera 2013; Legendre 2014), or even extended to functional and phylogenetic dissimilarity (Leprieur *et al.* 2012; Villeger, Grenouillet & Brosse 2013; Cardoso *et al.* 2014). For brevity and consistency with the terminology used by Legendre (2014), we will use the terms BAS and POD frameworks to refer to the original (Baselga 2010b) and alternative (Podani & Schmera 2011; Carvalho, Cardoso & Gomes 2012) partitioning methods. We however reserve the term ‘family’ for the set of measures derived from either Jaccard or Sørensen indices (i.e. Sørensen and Jaccard families as originally termed by Baselga 2012; Baselga & Orme 2012). From the introduction of POD framework (Podani & Schmera 2011; Carvalho, Cardoso & Gomes 2012), a debate has been developing, dealing with the meaning and relative advantages of each method.

Legendre (2014) reviewed the meaning and interpretation of the respective components of both BAS and POD approaches concluding that (i) it is the numerators of indices that estimate replacement and richness difference, (ii) the methodological discussion gravitates around the denominators, (iii) all denominators can be used, although ‘the chosen denominators might create distortions in the positioning of sites in an ordination’, (iv) alternative methods account for different concepts (replacement and nestedness vs. replacement and richness difference), and (v) none of the indices depend on the species richness of the two sampling units that are compared, provided that the proportion of shared species with respect to the species richness at each site remains the same. Legendre’s review clarified that the nestedness-resultant component (Baselga 2010b) and the richness-difference component (Podani & Schmera 2011; Carvalho, Cardoso & Gomes 2012) are intended to reflect different ecological concepts. Following this line of thought, because both approaches additively partition the same index, and because the second component reflects different concepts in BAS and POD frameworks (nestedness-resultant dissimilarity or richness difference, respectively), both

facts suggest that the first component (‘replacement’) cannot possibly reflect the same concept in either alternative method. Put it in logical terms, if $A = B + C = D + E$ and $B \neq D$, then it follows that $C \neq E$. Therefore, because we concur with Legendre’s view that each index must have a clear ecological interpretation, we here aim to (i) assess the differences between parallel components in alternative approaches (replacement vs. replacement and nestedness-resultant vs. richness difference), with special focus on the replacement components; (ii) test whether the replacement components derived from BAS and POD frameworks are independent of richness difference; (iii) evaluate whether tests of monotonicity between indices and ecological processes are informative to assess the performance of indices; and (iv) illustrate the practical consequences of differences between BAS and POD frameworks using the North American freshwater fish fauna as an empirical example. Using the two frameworks, we aim to assess of the relative importance of geographical, ecological and historical factors in explaining beta diversity patterns in North American freshwater fish assemblages.

Methods

COMPARISON OF PARALLEL COMPONENTS

We compared the behaviour of indices derived from BAS and POD frameworks focusing on pairwise dissimilarity indices for presence–absence data, including both the Sørensen and Jaccard families. Equations for all indices are shown in Table 1. To compare indices under all possible situations, we first used an artificial data set including all possible combinations of the matching components a , b and c , where a is the number of species present in both sites, b is the number of species present in the first site, but not in the second, and c is the number of species present in the second site, but not in the first. To do this, we built a table with the 501 501 combinations of a , b , c components given that

Table 1. Overview of the pairwise dissimilarity measures mentioned in this article, including names, notation, formulas and references

Family	Framework	Measure	Notation	Legendre’s notation	Formula	References
Jaccard	BAS	Jaccard dissimilarity	β_{jac}	D_J	$\frac{b+c}{a+b+c}$	Jaccard (1912); Koleff, Gaston & Lennon (2003)
		Turnover component of Jaccard dissimilarity	β_{jtu}	$Repl_{BJ}$	$\frac{2*\min(b,c)}{a+2*\min(b,c)}$	Baselga (2012)
		Nestedness-resultant component of Jaccard dissimilarity	β_{jne}	Nes_{BJ}	$\frac{ b-c }{a+b+c} * \frac{a}{a+2*\min(b,c)}$	Baselga (2012)
	POD	Williams replacement index	β_{-3}	$Repl_J$	$\frac{2*\min(b,c)}{a+b+c}$	Williams (1996); Podani & Schmera (2011); Carvalho <i>et al.</i> (2013)
Sørensen	BAS	Richness-difference component of Jaccard dissimilarity	β_{rich}	$Rich_J$	$\frac{ b-c }{a+b+c}$	Podani & Schmera (2011); Carvalho <i>et al.</i> (2013)
		Sørensen dissimilarity	β_{sor}	D_S	$\frac{b+c}{2a+b+c}$	Sørensen (1948); Koleff, Gaston & Lennon (2003)
		Simpson dissimilarity (=turnover component of Sørensen dissimilarity)	β_{sim}	$Repl_{BS}$	$\frac{\min(b,c)}{a+\min(b,c)}$	Simpson (1943); Lennon <i>et al.</i> (2001); Koleff, Gaston & Lennon (2003)
	POD	Nestedness-resultant component of Sørensen dissimilarity	β_{sne}	Nes_{BS}	$\frac{ b-c }{2a+b+c} * \frac{a}{a+\min(b,c)}$	Baselga (2010)
		Legendre replacement index	$\beta_{-3,s}$	$Repl_S$	$\frac{2*\min(b,c)}{2a+b+c}$	Legendre (2014)
		Legendre richness-difference index	$\beta_{rich,s}$	$Rich_S$	$\frac{ b-c }{2a+b+c}$	Legendre (2014)

regional richness (i.e. both sites taken together) equals to 1000 species (i.e. $a+b+c = 1000$). Based on this data set, we computed the dissimilarity components derived from BAS and POD frameworks, using package *betapart* (Baselga & Orme 2012) and *ad hoc* code, respectively. We here use the original notation (based on Koleff, Gaston & Lennon 2003) to refer to each index (see Table 1), plus two new abbreviations following the same format for the replacement and richness-difference components of Sørensen index introduced by Legendre (2014): $\beta_{-3,s}$ and $\beta_{rich,s}$, respectively. We plotted each component in BAS framework against the analogous component in POD framework (replacement vs. replacement and nestedness-resultant vs. richness difference). To illustrate mismatches between parallel components derived from BAS and POD frameworks, a set of particular cases was superimposed to the plots, aiming for an interpretation of the differences.

DEPENDENCE ON RICHNESS DIFFERENCE

To test whether replacement components derived from BAS and POD frameworks are statistically independent of richness difference, we adopted the *random parameter approach* described by Chao, Chiu & Hsieh (2012). In short, this approach considers that the variables (replacement and richness difference in this case) are random variables and values are simulated from a uniform distribution. If two uniform random variables are independent, we only need to check whether the set of all possible values that the two variables can jointly take forms a rectangle in a two-dimensional plane (Chao, Chiu & Hsieh 2012). We thus plotted all the components derived from BAS and POD frameworks against the absolute richness difference between sites (i.e. $|b-c|$). Again, to illustrate mismatches between parallel components derived from BAS and POD, a set of particular cases was superimposed to the plots.

To formally test the independence of BAS and POD replacement components from richness difference, we also computed the marginal and joint probabilities of random events involving pairs of values of richness difference and replacement indices. We selected two random P values between 0.01 and 0.99 (i.e. pR and $p\beta$) and computed the quantile of richness difference corresponding to pR (qR), as well as the quantile of the replacement dissimilarity index corresponding to $p\beta$ ($q\beta$). The joint probability of richness difference $<qR$ and replacement index $<q\beta$ was computed empirically as the proportion of pairs of values in which richness difference was lower than qR , and the replacement index was lower than $q\beta$. If the dissimilarity index is independent of richness difference, the joint probability of a pair of random events ($pR\beta$) should be equal to the product of the marginal probabilities ($pR \cdot p\beta$). This procedure was repeated 1000 times for random values of pR and $p\beta$, and for the 4 replacement indices (β_{-3} , $\beta_{-3,s}$, β_{TU} and β_{sim}).

MONOTONICITY BETWEEN INDICES AND PROCESSES

Because the tests of monotonicity between indices and processes in which species are replaced and/or lost have been used to assess the respective merits of BAS and POD frameworks (Carvalho *et al.* 2013; Legendre 2014), we here introduce alternative simulations to evaluate whether tests of monotonicity are suitable ways to assess the behaviour of indices. First, we reproduced the simulation reported by Carvalho *et al.* (2013), in which an original assemblage with 100 species suffers one species replacement and 3 species losses each time step (i.e. $a-4$, $b+1$, $c+4$ at each step), for 25 steps in total ('replacement and loss' scenario, Fig. S1a in Appendix S1). In this case, the dissimilarity between the assemblage at each step and the original one was computed. A second simulation involved two islands, one richer (125 species) than the

other (35 species), and 25 species in common. Using again 25 time steps, we made one species common to both islands to go extinct in the poorest island (thus becoming unique to the richest island) each time, that is $a-1$, $b+0$, $c+1$ at each step ('extinction' scenario, Fig. S1b in Appendix S1). The dissimilarity between both island assemblages was measured at each time step. A third simulation involved two islands, one richer (60 species) than the other (35 species) and 10 species in common. One unique species of each island colonizes the other island each time, that is $a+2$, $b-1$, $c-1$ at each step ('homogenization' scenario, Fig. S1c in Appendix S1). A fourth simulation involved two islands, one of them with 100 species, the other one with no species at all. Using again 25 time steps, we allowed four species from the first island to arrive to the second one each time. Two of these four colonizing species also remained in the first island, while the other two became extinct in the first island, becoming thus unique to the second one, that is $a+2$, $b-4$, $c+2$ at each step ('colonization and extinction in source' scenario, Fig. S1d in Appendix S1). The dissimilarity between both island assemblages was measured at each time step. In the four simulations, we computed Jaccard dissimilarity and its components, as derived from BAS and POD frameworks, and plotted the indices against time steps. Again, to illustrate the reasons of the observed trends, we added to the plots the corresponding combinations of a , b and c matching components every five steps.

EMPIRICAL BETA DIVERSITY PATTERNS IN THE NORTH AMERICAN FRESHWATER FISH FAUNA

Likewise, we assessed the implications of the reported differences between components derived from BAS and POD frameworks for empirical studies using the North American freshwater fish fauna as a case study. Specifically, we assessed the relative importance of (i) geographical distance, (ii) differences in contemporary environmental conditions and (iii) differences in glacial history in shaping freshwater fish dissimilarity patterns. To do so, we compiled information on the distribution of native and strictly freshwater fish species ($n = 549$) across 171 river basins distributed in USA (including Alaska) and Canada (see Brosse *et al.* 2013 for data sources) and the corresponding spatial and environmental predictors (see methods in Appendix S1 in Supporting Information).

We applied simple Mantel tests and multiple regression on distance matrices (MRM, Legendre, Lapointe & Casgrain 1994) to assess the relationships between assemblage dissimilarity and (i) geographical distance, (ii) differences in contemporary environmental conditions and (iii) differences in glacial history in shaping freshwater fish dissimilarity patterns. For a given explanatory variable, calculation of the standardized partial regression coefficients (β) enabled us to compare their per-unit effect on compositional dissimilarity, while controlling for the effect of the other variables. To overcome the problem of lack of independence between site pairs, the significance of the standardized partial regression coefficients and the coefficients of multiple determination (R^2) was assessed using a permutation test ($n = 999$). These analyses were performed using the *ecodist* package in R (Goslee & Urban 2007). Only MRM results are presented in the main text as simple Mantel tests provided similar results (see Table S2 in Appendix S1).

Results

COMPARISON OF PARALLEL COMPONENTS

Relationships between analogous components in BAS and POD frameworks turned out to be triangular (Fig. 1). This

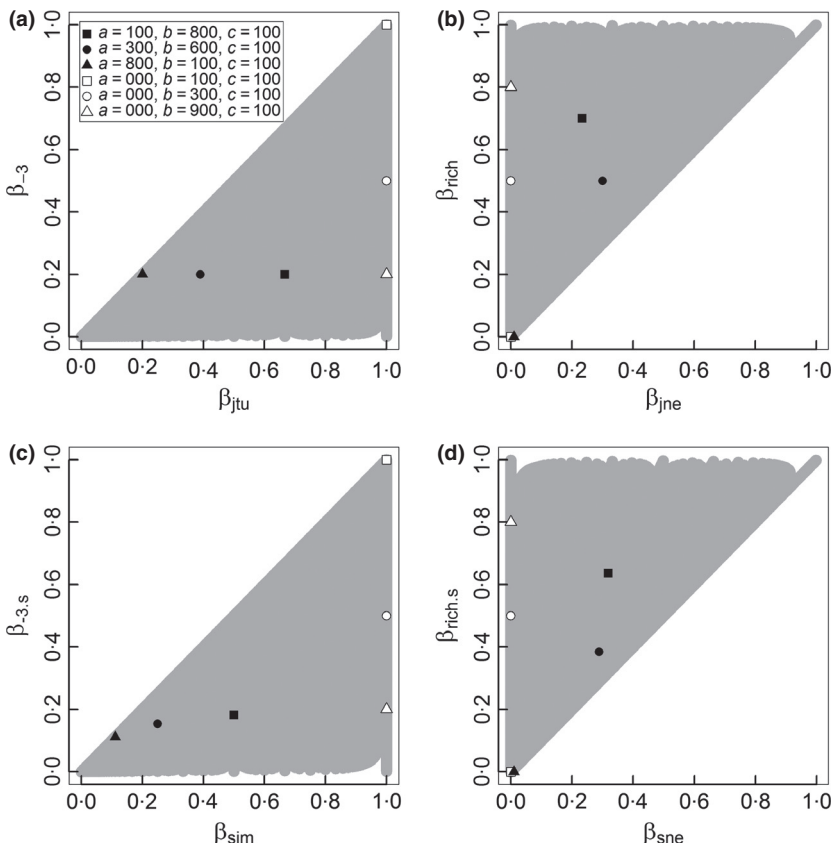


Fig. 1. Relationship between parallel components in BAS and POD partitioning frameworks derived from all possible combinations of matching components for $a+b+c = 1000$. The replacement vs. replacement (a, c) and nestedness-resultant vs. richness-difference components (b, d) are plotted (grey dots) for the Jaccard (a, b) and Sorensen families (c, d). To facilitate interpreting discrepancies between indices, special cases are highlighted as black [increasing a , decreasing $\max(b,c)$, constant $\min(b,c)$] and white symbols [constant a , increasing $\max(b,c)$, constant $\min(b,c)$]. Note that the latter (white symbols) represent cases where $a+b+c \neq 1000$ to exemplify the simple pattern of adding species to the richest site. The situations in white squares and circles are strictly equivalent to $a = 0$, $b = 500$, $c = 500$ and $a = 0$, $b = 750$, $c = 250$, respectively. Black triangles are slightly displaced to the right to improve visualization in (b) and (d).

result is unsurprising for the comparison of the nestedness-resultant component from BAS framework against the richness-difference component from POD framework (Fig. 1b, d). Indeed, as pointed in previous contributions, while the nestedness-resultant component quantifies differences in species richness between assemblages nested to some degree (Baselga 2010b, 2012), the richness-difference component quantifies any difference in richness, irrespective of assemblages being nested or not (Podani & Schmera 2011; Carvalho, Cardoso & Gomes 2012). They thus quantify different concepts (Legendre 2014) and should not be interpreted as equivalent. The particular cases highlighted in Fig. 1b, d clearly exemplify the differences in behaviour. Because the nestedness-resultant component in BAS framework depends both on richness difference and the degree of nestedness, the index takes a constant value of zero when nestedness equals zero (i.e. no species in common), irrespective of richness difference (i.e. white symbols in Fig. 1b, d). In contrast, the richness-difference component in POD framework varies as a function of richness difference, irrespective of assemblages being nested to some degree, or not (circles in Fig. 1b, d).

The same type of triangular relationship was observed between the replacement components derived from either BAS or POD frameworks (Fig. 1a, c). This outcome was expected because if the nestedness-resultant and richness-difference components reflect different concepts, then the replacement components in either framework must reflect different concepts too. This is clearly exemplified by the highlighted particu-

lar cases in Fig. 1a, c. In the special case when there are no species in common, the replacement component in BAS framework remains at its maximum irrespective of richness differences (white symbols in Fig. 1a, c), while it decreases with richness differences in POD framework, irrespective of the fact that no species are shared between assemblages. On the other hand, when the number of unique species in the poorest site remains constant (black symbols in Fig. 1a, c), the replacement component in the BAS framework decreases with the increment of shared species, while the replacement component in the POD framework remains constant (Fig. 1a) or almost constant (Fig. 1c), as also shown in Baselga (2012: figure 3).

DEPENDENCE ON RICHNESS DIFFERENCE

As a result of the aforementioned differences, the replacement component in the BAS framework showed no relationship with richness difference (both β_{jtu} and β_{sim} , see Fig. 2e, g), while the replacement component in POD framework showed a negative triangular relationship with richness difference (both β_{-3} and $\beta_{-3,s}$, see Fig. 2a, c). Thus, as illustrated by the highlighted particular cases, in the BAS framework, the replacement component is quantified (i) to be at its maximum (=1) when no species are shared (irrespective of richness differences, squares in Fig. 2), (ii) at its minimum (=0) when the poorest site is nested in the richest site (triangles in Fig. 2), and, more generally, (iii) it is quantified to remain unchanged provided that proportion between the number of unique

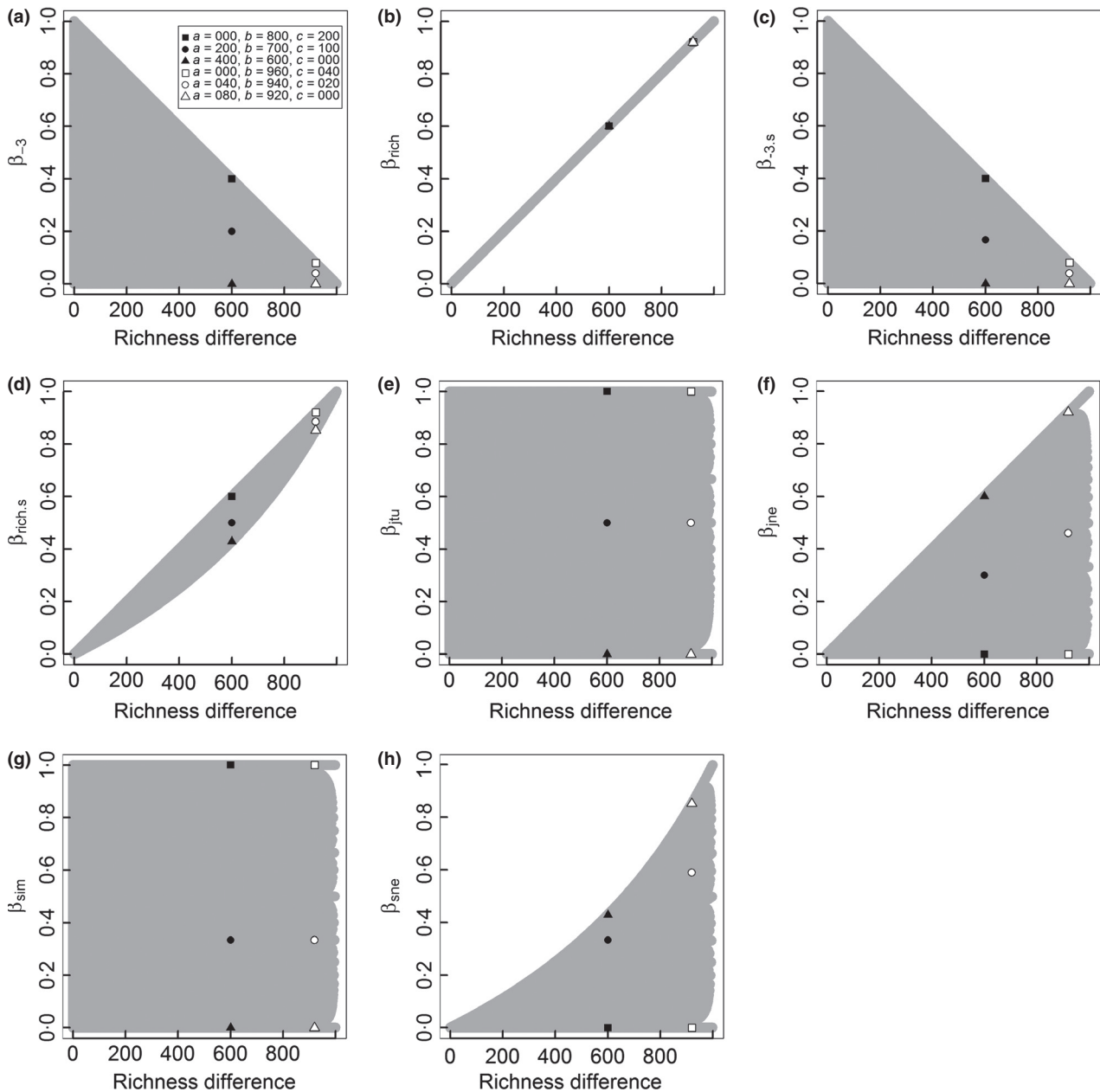


Fig. 2. Relationship between dissimilarity indices derived from POD (a–d) and BAS (e–h) partitioning frameworks, for all possible combinations of matching components for $a+b+c = 1000$. The components of Jaccard (a–b and e–f) and Sørensen dissimilarity (c–d and g–h) are shown. To facilitate interpreting discrepancies between indices, specific cases are highlighted as black [lower richness difference] and white symbols [higher richness difference].

species in the poorest site and the number of shared species remains constant (circles in Fig. 2, for which this proportion is 0.5 in both cases). In contrast, in the POD framework, the replacement component does depend on richness difference so, although it takes a zero value when both assemblages are perfectly nested, when nestedness is not perfect it decreases with richness difference despite the proportion between the number of unique species in the poorest site and the number of shared species remains constant (circles in Fig. 2) or even if no species are shared at all (squares in Fig. 2). The formal assessment confirmed the independence from richness differ-

ence of β_{jtu} and β_{sim} , but not of β_{-3} and $\beta_{-3,s}$ (Fig. 3). Joint probabilities of pairs of richness difference and dissimilarity values were extremely close to the product of their marginal probabilities for indices of the BAS framework (mean absolute difference was 0.00039 for both β_{jtu} and β_{sim}), and the distribution of differences was centred at zero (see histograms in Fig. 3). In contrast, differences between joint probabilities and the product of marginal probabilities for indices of the POD framework were two orders of magnitude larger (mean absolute difference was 0.039 and 0.029 for β_{-3} and $\beta_{-3,s}$, respectively) and biased towards negative values.

MONOTONICITY BETWEEN INDICES AND PROCESSES

When the respective behaviours of indices were tested under sequential scenarios of species substitution and loss (or gain), it turned out that monotonicity (or lack of it) depended on the particular conditions of the simulated process (Fig. 4). Thus, while scenario 1 (species replacement and loss, Fig. 4a) yielded a pattern of monotonic variation for both components of the POD framework, but not for the nestedness-resultant component of the BAS framework, scenarios 2 (colonization, Fig. 4b) and 3 (homogenization, Fig. 4c) generated the opposite outcome, that is a monotonic variation for both components of the BAS framework, but not for the replacement or the richness-difference components of the POD framework, respectively. Under certain conditions, as scenario 4 (colonization and extinction from source, Fig. 4d), none of the indices changed monotonically through all the steps of the process.

EMPIRICAL BETA DIVERSITY PATTERNS IN THE NORTH AMERICAN FRESHWATER FISH FAUNA

We applied the BAS and POD frameworks to an empirical data set describing the distribution of North American freshwater fishes across drainage basins. According to the Jaccard dissimilarity index (total beta diversity), half of the pairs of drainage basins have no species in common (median $\beta_{jac}=1$, see Table 2) hence indicating that these basins have completely different freshwater fish faunas. The replacement component of the BAS framework (β_{jtu}) showed a similar pattern (median $\beta_{jtu}=1$, Table 2), as $\beta_{jtu}=1$ when $a = 0$, that is species

replacement is at its maximum when no species are shared. In contrast, the replacement component of the POD framework indicated a low level of species replacement for most of the pairwise comparisons (median $\beta_{-3} = 0.235$, Table 2). In other words, according to the POD framework, the level of species replacement is low even between drainage basins with no species in common. According to the nestedness component of the BAS framework (β_{jne}), dissimilarities between nested fish faunas are very weak (median $\beta_{jne}=0$, Table 2), which is not surprising given that half of the pairs of drainage basins have no species in common. In contrast, the richness component of the POD framework revealed large differences in species richness between drainage basins (median $\beta_{rich}=0.666$).

A simple regression model based on distance matrices showed that species richness differences explained 27% of the variation in β_{-3} ($r^2 = 0.27$, $P < 0.001$) but only explained 4% of the variation in β_{jtu} ($r^2 = 0.04$, $P = 0.033$). Regression models testing the combined effects of geographical, ecological and historical distance-based variables on the components of the BAS framework accounted for 28.3%, 29.1% and 16.1% of the variation in β_{jac} , β_{jtu} and β_{jne} , respectively (Table 3). Partial standardized regression coefficients indicated that each of the considered distance-based variables was positively associated with total beta diversity as measured by β_{jac} . Similar results were found for β_{jtu} , at the exception that differences in surface area between drainage basins did not influence the level of species replacement. In contrast, β_{-3} showed markedly different results as species replacement was found to decrease with increasing differences in climatic conditions between drainage basins (Table 3). In addition, the regression model based on β_{-3} did not reveal a significant effect of glacial history on the level of species replacement. It is also worth noting that the

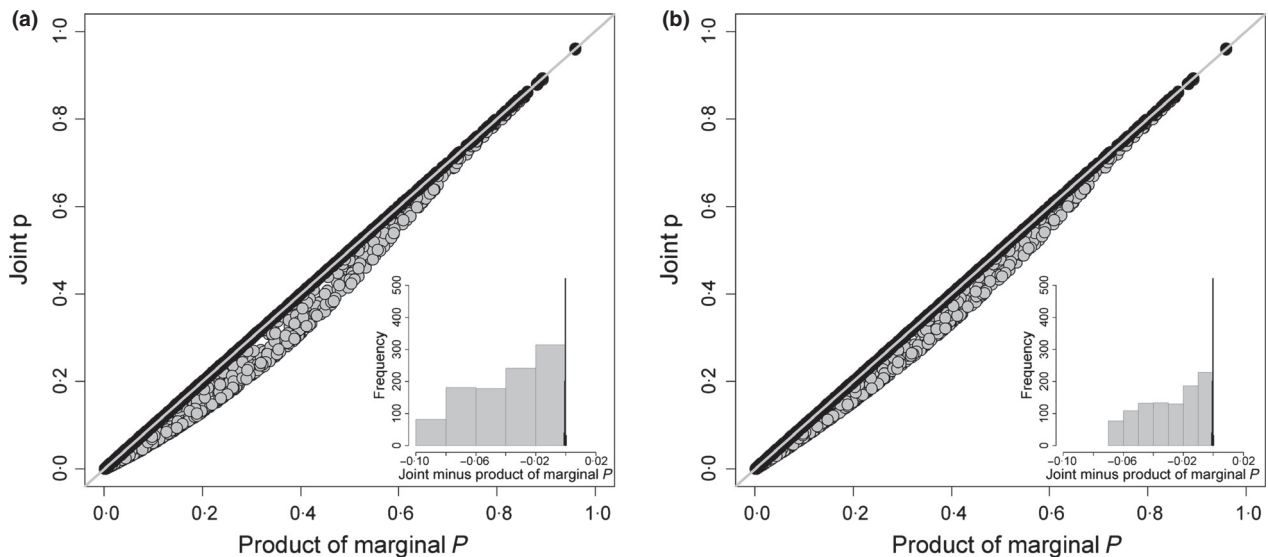


Fig. 3. Relationship between joint probability and the product of marginal probabilities of pairs of values of richness difference and replacement dissimilarity. (a) Dissimilarity is the replacement component of Jaccard family in the BAS (black dots) and POD (grey dots) frameworks. (b) Dissimilarity is the replacement component of Sørensen family in the BAS (black dots) and POD (grey dots) frameworks. The diagonal lines mark the 1:1 relationship (perfect fit between joint p and the product of marginal p). Histograms show the distribution of differences between joint p and the product of marginal p for BAS (black) and POD (grey) frameworks.

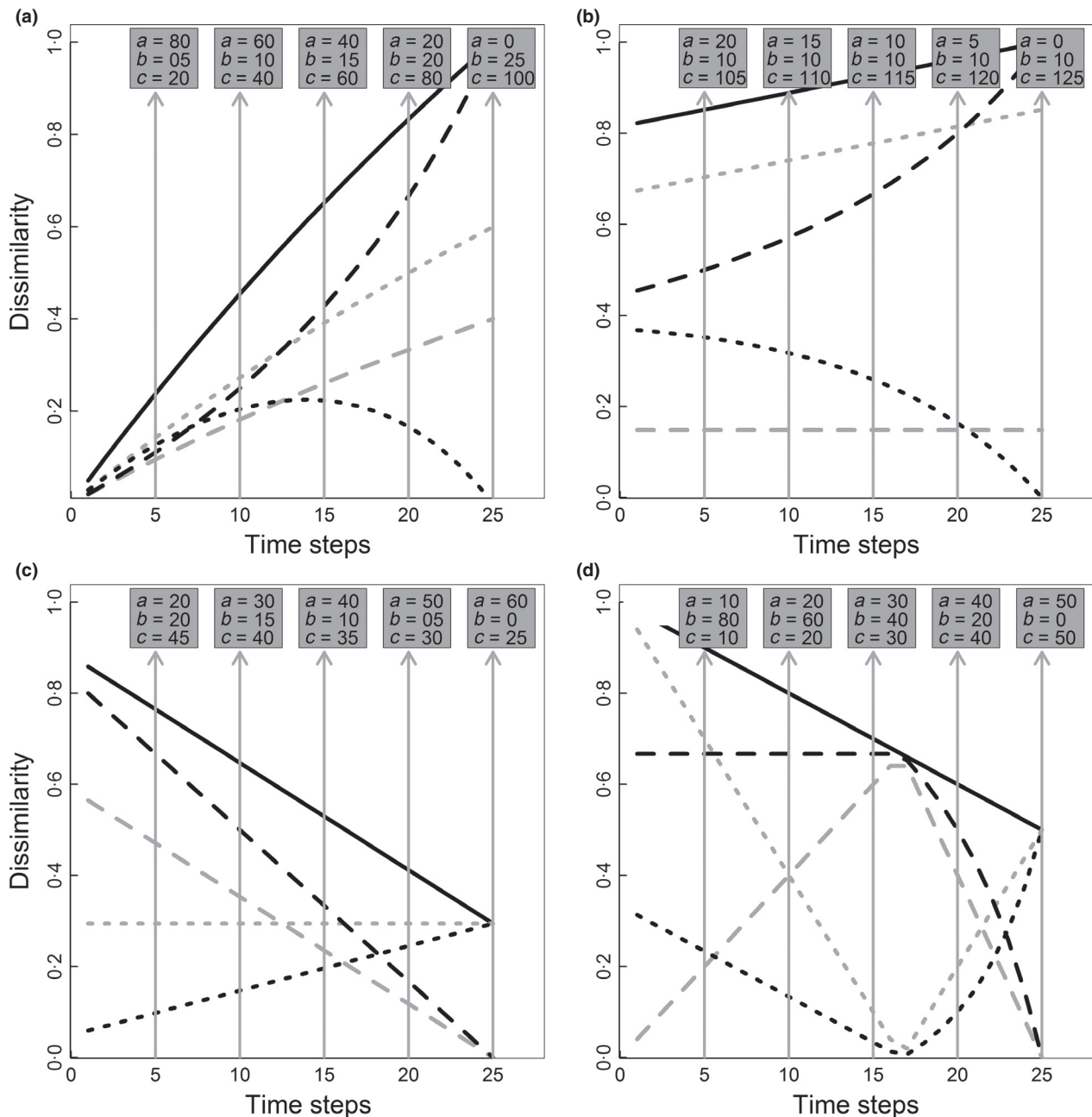


Fig. 4. Behaviour of indices derived from BAS and POD frameworks for the Jaccard family under four different simulations involving 25 steps: (a) simulation of a ‘replacement and loss’ scenario, described as Scenario 3 in Carvalho *et al.* 2013, that is $a-4, b+1, c+4$ at each step; (b) simulation of a ‘extinction’ scenario, in which $a-1, b+0, c+1$ at each step; (c) simulation of a ‘homogenization’ scenario, in which $a+2, b-1, c-1$ at each step) and (d) simulation of a ‘colonization and extinction in source’ scenario, in which $a+2, b-4, c+2$ at each step. The actual values of a, b and c matching components are shown every five steps to facilitate interpretation of trends. Jaccard dissimilarity (β_{jac}) is represented as a black solid line. The indices derived from the BAS framework are represented by black broken lines: black dashed line is the replacement (β_{repl}), and black dotted line is the nestedness-resultant component (β_{nec}). The indices derived from the POD framework are represented by grey broken lines: grey dashed line is the replacement (β_{-3}), and grey dotted line is the richness-difference component (β_{rich}).

regression model only explained 3.4% and 7.9% of the variation in β_{-3} and β_{rich} , respectively (Table 3).

Discussion

Our results show that, in exactly the same way that the nestedness-resultant and richness-difference dissimilarities account

for different concepts, the replacement dissimilarity indices derived from BAS and POD frameworks also account for different concepts. Related to this, the replacement component in the BAS framework is independent of richness difference, while the replacement component in the POD framework is not. It is thus inappropriate to use the same term (i.e. replacement) for indices that account for different concepts. In our view,

replacement (and those related ones as turnover, species substitution) should be reserved to those indices that are independent (i.e. not mathematically constrained) from richness difference. These are the Simpson index of dissimilarity (Simpson 1943; Lennon *et al.* 2001) and the turnover component of Jaccard dissimilarity (Baselga 2012), as well as their abundance-based (Baselga 2013; Legendre 2014), phylogenetic (Leprieur *et al.* 2012) and functional versions (Villegger, Grenouillet & Brosse 2013). In turn, a new name should be given to those indices depending both on species replacement and richness difference, as those derived from the POD framework (Podani & Schmera 2011; Carvalho, Cardoso & Gomes 2012; Cardoso *et al.* 2014; Legendre 2014).

Besides the terminological debate, our results help understanding the differences among indices and the concepts they account for. Despite Legendre (2014) view, our systematic comparison of indices points out that it is not the numerators of indices that estimate replacement and richness difference. The behaviour of indices, and thus the concepts they account for, depends on both the numerator and denominator. In consequence, denominators should not merely be considered as a way to relativize or standardize the measures, because they do introduce different meanings into indices. This is obvious if dissimilarities are transformed into similarities. Given the strict equivalence of similarity = 1 – dissimilarity, when the replacement indices derived from the POD framework are expressed as similarity indices, it turns out that the numerator now

cannot be expressed without including the richness difference $|b-c|$. For example, the replacement component for the Jaccard family in POD framework, β_{-3} is formulated as a similarity index as follows:

$$1 - \beta_{-3} = \frac{a + b + c}{a + b + c} - \frac{2 * \min(b, c)}{a + b + c} = \frac{a + |b - c|}{a + b + c}.$$

In contrast, the BAS framework shows that similarity for the replacement component can be expressed without including the richness difference $|b-c|$, exactly as its dissimilarity counterpart:

$$1 - \beta_{\text{itu}} = \frac{a + 2 * \min(b, c)}{a + 2 * \min(b, c)} - \frac{2 * \min(b, c)}{a + 2 * \min(b, c)} = \frac{a}{a + 2 * \min(b, c)}.$$

It should be stressed that (i) similarity and dissimilarity versions of a given index express exactly the same information (i.e. concept), and (ii) in both frameworks similarity and dissimilarity are expressed using the same denominator. Therefore, if it were the numerators that estimate replacement, it would turn out that the replacement component in the POD framework, when expressed as a similarity, would be determined by the number of species in common plus richness difference. In fact, it is the combination of numerator and denominator that provides a meaning to the index and, as shown by simulations, richness difference influences both components in the POD, but not in the BAS framework. For this reason, even in the absence of shared species (i.e. $a = 0$), the replacement component in the POD framework decreases with increasing richness difference (see also Leprieur & Oikonomou 2014), while it remains constant at its maximum in the BAS framework (white symbols in Fig. 1, squares in Fig. 2). More generally, for any fixed number of shared species, in the BAS framework the replacement component remains constant when species are added to the richest assemblage, while it decreases with increasing richness difference in the POD framework (Baselga 2012: figure 2).

So, how does this reconcile with Legendre (2014) proof that all components in BAS and POD frameworks are independent of species richness (property P10 in Legendre & De Cáceres 2013)? The compliance with property P10 of all the indices dis-

Table 2. Summary statistics for compositional dissimilarity between pairs of freshwater fish assemblages of North American river basins, measured as Jaccard dissimilarity and its components according to the BAS and POD frameworks

	β_{jac}	β_{itu}	β_{jne}	β_{-3}	β_{rich}
Min	0	0	0	0	0
Percentile 5%	0.600	0	0	0	0
1st Quartile	0.926	0.777	0	0.077	0.344
Median	1	1	0	0.235	0.666
Mean	0.926	0.826	0.100	0.318	0.608
3 rd Quartile	1	1	0.075	0.500	0.884
Percentile 95%	1	1	0.665	0.879	0.967
Max	1	1	0.995	1	0.995

Table 3. Results of multiple regression on distance matrices assessing the relative effects of geographical, ecological and historical factors in shaping compositional dissimilarity patterns in the North American freshwater fish fauna

Variables	Partial standardized regression coefficients (β_{jac})	Partial standardized regression coefficients (β_{itu})	Partial standardized regression coefficients (β_{jne})	Partial standardized regression coefficients (β_{-3})	Partial standardized regression coefficients (β_{rich})
Geographical distance	0.212***		0.197***		–0.007
Surface area	0.115***	–0.017		0.107***	0.109***
Altitude	0.047**	0.095***		–0.100***	0.038*
Climate PCA1	0.176***	0.134***		–0.062*	0.1914***
Climate PCA2	0.203***	0.234***		–0.183***	0.004
Glacial history	0.184***	0.229***		–0.190***	0.084***
R^2	0.283***	0.291***		0.161***	0.079***

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

cussed here was expected, as they are components of Jaccard and Sørensen dissimilarities, which themselves are monotonic transformations of multiplicative beta diversity, which is independent of alpha and gamma diversity (Jost 2007; Baselga 2010a; Chao, Chiu & Hsieh 2012). Legendre (2014) proof thus applies for the dependence of dissimilarities on mean (alpha) or total (gamma) species richness, but not on richness difference between sites. The compliance with P10 implies that all indices remain unchanged if the proportions of the a , b and c components remain constant (e.g. table S1.6 in appendix S1 of Legendre 2014). This is a highly relevant property, also known as the 'replication principle' (Ricotta 2008), which is, for example, not fulfilled by Euclidean distance (Legendre & De Caceres 2013) because this index is related to additive beta diversity, which is constrained by alpha and gamma diversity (Jost 2007; Baselga 2010a; Chao, Chiu & Hsieh 2012). However, the property we are discussing here is a different one and refers to the independence of the replacement component on the difference in species richness between sites $|b-c|$ and not on total richness ($a+b+c$). In table S1.6 of Legendre 2014, all indices remain unaffected by changes in richness difference because these changes are derived from changes in total richness. If we keep total richness constant and consider all possible combinations in a , b and c , it turns out that the replacement component in the BAS framework (i.e. β_{Jtu} and β_{sim} , for the Jaccard and Sørensen families, respectively) is independent of richness difference, while the replacement component in the POD framework (i.e. β_{-3} and $\beta_{-3,s}$, for the Jaccard and Sørensen families, respectively) is not. This means that if a correlation between richness difference and the replacement component of the BAS framework is observed in an empirical data set, this would reflect a meaningful ecological pattern and not a methodological constraint. In contrast, if a correlation between richness difference and the replacement component of the POD framework is observed in an empirical data set, it would be impossible to know if this is a meaningful ecological pattern or just a methodological bias derived from the fact that the replacement index is mathematically constrained by richness difference.

The aforementioned differences in behaviour between the respective components of BAS and POD frameworks make them respond monotonically or not with respect to different processes in each case. For example, the nestedness-resultant component of the BAS framework does not monotonically respond to the 'replacement and loss' simulation, and the reason for this is that as the process goes on, nestedness is reduced, to finish with no species in common (i.e. $a = 0$). This behaviour is indeed expected for an index that quantifies the dissimilarity caused by richness difference in nested subsets. On the other hand, the simulated 'extinction' process shows that the replacement component of the POD framework does not increase monotonically, while (i) the number of shared species decreases and (ii) the number of unique species in the poorest site and the total number of species remain constant (see Fig. 4b). In our view, this is inconsistent with the concept of replacement. However, the major point we want to stress with alternative simulations is that the monotonicity of indices against pro-

cesses depends on the particular processes being simulated and that it is possible to imagine simple ecological processes in which none of the indices show a monotonic behaviour. There is nothing wrong with this, as the relevant point here, in our view, is that indices do quantify patterns, not processes. Patterns may be used to infer processes, but it is well known that different processes can generate identical biodiversity patterns (Currie *et al.* 2004; Currie 2007) and, more specifically, identical dissimilarity values can be the result of different processes (i.e. extinction, speciation, colonization). Therefore, it is unrealistic to expect that any index shows a monotonic relationship with any combination of the processes potentially behind the patterns we measure.

In empirical studies, the consequences of using one or another framework may be remarkable, and more particularly when the number of shared species is very low between the studied localities and when species richness differences are large. Indeed, our results for North American freshwater fish assemblages showed that, using the BAS framework, the species replacement component is perceived as the dominant contributor to fish compositional dissimilarity between drainage basins. In contrast, using the POD framework, the richness-difference component was found to contribute mainly to fish compositional dissimilarity. The fact that both frameworks make contrasting estimations of the contribution of species replacement to total beta diversity can have marked consequences when assessing the relative influence of geographical, ecological and historical factors in shaping beta diversity patterns. For instance, the BAS framework uncovers the importance of past glaciation events in explaining present-day patterns of species replacement in the North American freshwater fish fauna. This is in accordance with the well-known effect of Quaternary glaciations on the distributions of North American freshwater fishes (Leprieur *et al.* 2011; Ross & Matthews 2014). The POD framework was unable to reveal this striking pattern, as according to this method species replacement was not greater between drainage basins with different glacial histories than between drainage basins with similar glacial histories. Such discrepancies in the results obtained using the BAS and POD frameworks are directly related to the fact the replacement component of the POD framework (i) is strongly influenced by species richness differences (see Table S2 in Appendix S1 for this case study) and (ii) violates the complementarity property (e.g. Clarke, Somerfield & Chapman 2006; Legendre & De Caceres 2013), namely that pairs of drainage basins with no species in common should have the largest dissimilarity and hence the maximal level of species replacement, whatever their differences in species richness.

Conclusions

Users may choose between BAS and POD frameworks based on the now well-known properties of both alternatives. As already noted by Legendre (2014), the nestedness-resultant and richness-difference components of BAS and POD frameworks, respectively, account for different concepts. We here have shown that the so-called replacement components of

BAS and POD frameworks do also account for different concepts. Therefore, both partitioning frameworks are only partially related, and quantify different properties of assemblages. For years, biogeographical studies emphasized the importance of analysing large-scale patterns of species replacement (or turnover) after having controlled for species richness differences (e.g. Simpson 1943; Harrison, Ross & Lawton 1992; Williams 1996; Koleff, Gaston & Lennon 2003; Baselga 2007; Leprieur *et al.* 2009; Kreft & Jetz 2010; Barwell, Isaac & Kunin 2015). By considering species richness differences in the denominator, the replacement component of the POD framework fails to fulfil this requirement. In turn, the richness-difference component of the POD framework can be considered as a useful tool to measure how dissimilar are assemblages in terms of species richness. However, this can in fact also be done using classical approaches that rely on direct measures of species richness (e.g. Araújo *et al.* 2008). In our view, variation in species richness can be directly assessed without using dissimilarity indices, while variation in species composition is better understood if partitioned using the BAS framework, which allows separating (i) the variation in species composition derived from species replacement which is independent of richness difference (i.e. not mathematically constrained by it) and (ii) the variation in species composition derived from nested patterns.

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Data accessibility

Biological and environmental data corresponding to the empirical case study (North American freshwater fish fauna) are available in Supporting Information (Data S1–S2).

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Supporting Information

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

Appendix S1. Supplementary methods and results.

Data S1. Presence/absence table for freshwater fish species in North American basins.

Data S2. Environmental data for North American basins.