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

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ABSTRACT

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

56 **Introduction**

57

58 Beta diversity has been interpreted mostly as the extent of change in community composition
59 (Whittaker 1960, Koleff et al. 2003) along a given gradient and may also be understood as
60 variation among sampling units without any specific reference to gradients (Anderson et al.
61 2011). In any case, beta diversity patterns are originated from two distinct processes, the
62 replacement and the loss (or gain) of species. Of the two, only the loss (or gain) of species
63 causes richness differences from site to site. When losses or gains occur in a more or less
64 ordered manner, community pattern becomes nested (Atmar and Patterson, 1993). In
65 general, nestedness refers to the extent to which species of a smaller assemblage are a
66 subset of a larger assemblage and is therefore a particular case of richness differences
67 (Almeida-Neto et al. 2008, Ulrich et al. 2009). In nature, the replacement and loss (or gain) of
68 species are combined in an infinite number of ways, leading to complex patterns of
69 community dissimilarity. Therefore, to understand the origins of beta diversity, nestedness
70 and their causes, one has to determine the relative roles of replacement and richness
71 differences.
72 The necessity of decomposing measures of beta diversity and nestedness into comparable
73 fractions is thus obvious. Indeed, the idea of partitioning beta diversity into different
74 components is not new. Several authors have used various measures with different properties
75 in order to differentiate the influence of replacement and species loss on the origins of beta
76 diversity (Harrison et al. 1992, Williams 1996, Lennon et al. 2001, Melo et al. 2009).
77 Nevertheless, none of these contributions established a comprehensive and unified
78 framework for partitioning beta diversity. Recently, several attempts have been made to
79 bridge this gap. The first one is due to Baselga (2010) proposed a general framework for
80 unifying the different components of beta, suggesting partitioning pairwise beta diversity
81 expressed by the Sørensen dissimilarity into replacement (turnover) and “nestedness
82 resultant” components. An alternative solution has also been proposed independently by
83 Podani and Schmera (2011) and Carvalho et al. (2012). In this, beta diversity is measured by
84 Jaccard dissimilarity which is decomposed into replacement and richness difference fractions.
85 The richness difference fraction is taken as a positive contributor to a nestedness measure

suggested by Podani and Schmera (2011). Even more recently, Baselga (2012) has rejected this suggestion and proposed decomposing Jaccard dissimilarity in the same fashion as the Sørensen index. Unfortunately, these different methods can lead to radically different conclusions about the same dataset (Carvalho et al. 2012) making inevitable the comparison of these approaches so that users of either approach can learn their relative merits and potential pitfalls and limitations.

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

Existing methods for partitioning beta diversity

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

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

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

β_{sor} - β_{sim} would yield a measure of dissimilarity due to nestedness (β_{nes}).

The performance of Baselga's (2010) method was found to be inconsistent with the variation of species replacement and species loss (Podani and Schmera 2011, Schmera and Podani 2011, Almeida-Neto et al. 2012, Carvalho et al. 2012). A new partitioning of beta diversity, due to Podani and Schmera (2011) and Carvalho et al. (2012) provides formal definitions of both absolute and relativized measures in terms of the parameters of the 2x2 contingency table (Table 1). Absolute beta diversity is expressed as b+c (Weiher - Boylen beta, see Koleff et al. 2003), which is divided into species replacement and richness difference fractions. The term replacement means that a species in one site is substituted by a species in another site (or point of time in the same site). Therefore, one replacement always involves two species and the total number of replaced species is equal to 2min(b,c). Richness differences arise from the loss (or gain) of species and are measured as |b-c|. Therefore, the contingency table can be algebraically decomposed into two biologically sound asymmetric components, according to the expression:

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

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

Relativization of beta diversity may be achieved by division with the total number of species of the system (n=a+b+c), which has an obvious theoretical link to the gamma diversity concept as applied to pairs of sites. Thus, we have the Jaccard dissimilarity β_{cc} (β_{jac} in Baselga' notation) which can be decomposed into relativized species replacement or dissimilarity due to replacement ($\beta_{-3,}$, or R_{rel} in Podani and Schmera's notation) and relativized richness difference or dissimilarity due to richness differences (β_{rich} or D_{rel}), as given below

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

Relativized nestedness (N_{rel}) is understood as the sum of Jaccard similarity (overlap) and

146 relativized richness difference, with the same condition as above. It is seen immediately that
147 there is a fraction shared by beta diversity and nestedness, namely richness difference, either
148 absolute or relativized (Podani and Schmera 2011, 2012, which may also be consulted for
149 other pairwise measures of nestedness and their comparative evaluation). Although, the
150 definition of nestedness differs with studies (Ulrich et al. 2009), our approach establishes a
151 conceptual and methodological link between beta diversity and nestedness, and facilitate
152 understanding and application of these measures in ecology and biogeography. (Note that we
153 did not give any decomposition related to Sørensen dissimilarity because double weighted
154 overlap scores in this coefficient do not apply to any meaningful definition of nestedness).
155 However, Baselga (2012) has rejected the above suggestions. Following the same rationale
156 he used for partitioning β_{sor} into replacement and nestedness-resultant dissimilarity, he
157 proposed a similar partitioning of β_{cc} into dissimilarity due to replacement (β_{jtu}) plus
158 dissimilarity due to nestedness (β_{jne}), such that:
159
160 $\beta_{cc} = \beta_{jtu} + \beta_{jne}$
161
162 (see Table 1).
163
164 **Theoretical issues**
165
166 *Scaling*
167 In comparing the alternative approaches, let us first examine the scaling of coefficients
168 involved in the decomposition of beta diversity. In the partitioning of β_{sor}, Baselga (2010)
169 scaled total dissimilarity (b+c) to the sum of species richness scores of both sites (2a+b+c),
170 whilst replacement (2min(b,c)) was scaled to what would be the species richness of each site
171 if "both sites were equally rich" (a + min(b,c)), resulting in the β_{sim} index. In the partitioning of
172 β_{cc}, Baselga (2012) scaled total dissimilarity (b+c) to the total number of species of the
173 pairwise system (a+b+c), whilst replacement (2min(b,c)) was scaled to the quantity
174 a+2*min(b,c) assumed to establish the "limit of the total number of species that could be
175 replaced at all". It is seen immediately that the replacement fractions implicitly included in β_{sor}

and β_{cc} are not mathematically and conceptually equivalent to the replacement given by β_{sim} and β_{jtu}, respectively.

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

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

By contrast, our approach offers easy interpretation of results both *mathematically* and *ecologically.* For the same example as above, the meaning of absolute values is straightforward: b+c=7 is the number of species not shared by the two sites (beta), 2min{b,c}=4 is species replacement and |b–c| = 3 is richness difference. By standardization with n (=10), we obtain the Jaccard index, β_{cc} = 7/10, relativized species replacement, β_{-3} = 4/10, and relativized richness difference component, β_{rich} = 7/10 – 4/10 = 3/10. In words, 7/10

205 is the proportion of the total number of species in which the two sites differ, 4/10 is species
206 turnover relative to the total number of species and 3/10 is the proportional difference in site
207 counts. Thus, there is a common currency for all component terms, both absolute and
208 relativized, therefore the algebraic relationship between total dissimilarity and species
209 replacement is maintained (Fig. 1) and the ecological meaning of all these terms is
210 straightforward.
211

212 *On maximum replacement*

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

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

232 • We do not see any reason why only the poorer site should establish the theoretical
233 upper limit of species replacement. It is therefore useful to examine under which

circumstances can a+2min(b,c) be the maximum. Assume first that the total number of species in the two sites is constant, so the theoretical maximum can only be determined by breaking up joint presences in the data. The use of a+2min(b,c) as denominator implies that maximum is reached when a/2 species remain only in site 1 and a/2 species in the other (Fig. 2.A and B). Complications may arise, of course, when “a” is an odd number. Nonetheless, the two sites can be “potentially” equally rich and replacement even higher if the set of shared species is split between the sites such that their richness difference is compensated for (Fig. 2.A and C). The extent to which this compensation is possible is determined by |b–c|, so that the maximum of species replacement can be higher than a+2min(b,c) and is in fact constrained by both sites whenever |b–c|>0. We can imagine another reasonable solution in which the number of species in each site remains constant and the total number of species increases. As seen in Fig. 2.D, in this case the maximum is 2a+2min{b,c}, larger than what Baselga (2012) proposed.

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

- The proposed replacement formula 2min(b,c)/(a+2min(b,c)) does not satisfy the requirements set up by Baselga (2012, p. 3, right column in the Early View document) himself, namely, that “adding unique species to only one of the sites should not affect the replacement measure”. If a new species is added to the species poorer site, then the replacement measure suggested by Baselga (2012) does change. (For example, for a=5, b=4, and c=1, we obtain 2/7, whereas for a=5, b=4 and c=2, we get 4/9). Addition of this new species clearly modifies the nominator and the denominator, thus the *proportion* of the species shared as well, so that the above requirement is in clear

conflict with the following one “any change in the proportion of species shared between two sites should be reflected by a meaningful measure of species replacement” (Baselga 2012, p. 3, right column in the Early View document). It was specified by Baselga (2012) as the second main property that a meaningful replacement function must have. Confusion around admissible properties of the replacement index probably came from the fact that in Fig. 1 of Baselga (2012) changes are monitored over increases of *n*, while *n* remains constant in his Fig. 2.

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

Decomposition of beta diversity in the absence of nestedness

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

a	**b**	**c**
j *k*	*j* *k*	*j* *k*
1 0	1 0	1 0
0 1	1 0	1 0
0 1	1 0	1 0
0 1	0 1	1 0
0 1	0 1	0 1
0 1	0 1	0 1
0 1	0 1	0 1
0 1	0 1	0 1

In all cases, $\beta_{sor} = \beta_{sim} = 1$ as well as $\beta_{cc} = \beta_{jtu} = 1$. However, in absolute terms beta diversity is dominated by richness difference in **a** (1 species replaced by another but *k* has six other species), richness difference and species replacement are more balanced in **b** (3 species are replaced by other 3 and *k* has two more species than *j*) and, finally, richness difference is

298 eliminated in **c** (both *j* and *k* have 4 species). That is, whenever (b≠c) > 0 and a = 0, absolute
299 beta diversity will have a fraction due to species replacement (i.e., 2min{b,c}) and another due
300 to richness difference (|b–c|), and so will do relativized beta diversity. Beta diversity can be
301 equated with species replacement only if b = c. Clearly, the indeterminate relationship
302 persists even if a>0. The conclusion is that the measure of beta diversity and its replacement
303 component should carefully be selected and that β_{sim} and β_{jtu} as defined in Baselga (2010,
304 2012, respectively) do not reflect properly the replacement component of beta diversity
305 quantified in either way, therefore β_{nes} and β_{jne} are meaningless. This basic problem of
306 Baselga's methods is illustrated in the small example of Fig. 3. β_{nes} and β_{jne} reveal a hump-
307 shaped relationship with increasing dissimilarity due to the loss of species and, hence, their
308 behaviour is not consistent with the concept that they try to express quantitatively.

309 To sum it up, if a = 0 and (b≠c) > 0 then beta diversity can still be partitioned into a
310 replacement and a richness difference component and these component names are also
311 valid, though nestedness does not exist. The conclusion is that even if beta diversity and the
312 replacement component are properly selected, it is incorrect to call their difference as
313 "nestedness resultant component", because nestedness does not necessarily exist when that
314 difference is larger than zero. Therefore, the ecologically meaningful term for this difference is
315 "richness difference", a term suggested independently by Podani and Schmera (2011) and
316 Carvalho et al. (2012).
317
318
319 **Testing the performance of different frameworks**
320
321 The performance of the different frameworks for decomposing beta diversity into additive
322 components was tested by a simulation study in which different gradients of dissimilarity, with
323 known degrees of species replacement and species loss, were created. We also examined
324 the behaviour of the different frameworks in the analysis of empirical data.
325
326 *A simulation study*
327 We created three artificial data sets modelling the temporal change of a given community

328 under different conditions. Each community initially had 100 species. At each time step, each
329 community suffered a predefined level of species replacement and species loss, according to
330 three scenarios. In scenario 1, we increased the number of replacements and the number of
331 losses by one at each step, therefore, species replacement > species loss (recall that one
332 replacement involves two species). In scenario 2, the number of replacements was set to one,
333 while the number of losses was set to two, hence species replacement = species loss. For
334 scenario 3, the number of replacements was set to one and the number of losses was set to
335 three, thus species replacement < species loss. We continued these processes for 25 steps
336 in time. For each data set, beta diversity measures were calculated at each step in
337 comparison to the initial state. Fig. 3 exemplifies the design of these simulations.
338 We advocate that an ecologically meaningful partitioning of beta diversity should obey two
339 basic expectations under the simulated conditions: i) any dissimilarity measure should
340 increase monotonically in each scenario, because total dissimilarity, species replacement and
341 species loss increase at every time step; ii) the ordering relationship between the measures
342 deemed to represent species replacement (β_{sim}, β_{jtu} and β_{-3}) and species loss (β_{nes}, β_{jne} and
343 β_{rich}) should be consistent with the proportion between the actual number of replacements and
344 species losses in the three scenarios. These are the most intuitive and uncontroversial
345 expectations that we can find. Any measure that does not satisfy these criteria would lead to
346 obviously wrong ecological conclusions and conservation decisions.
347 All calculations were performed in the R statistical environment (R Development Core Team
348 2011). The algorithm for the simulation and the calculation of all measures of beta diversity
349 can be found in Supplementary material Appendix 1.
350 The results of simulations reveal different behaviours of the beta diversity partitioning
351 methods (Fig. 4). Two functions, β_{nes} and β_{jne}, failed to satisfy the first requirement. These
352 measures exhibited a hump-shaped behaviour along with increasing loss of species, meaning
353 that when the loss of species is maximum, both measures give lower values than when
354 losses are intermediate. Regarding the second criterion, all the measures seem to be
355 consistent in scenario 1. For scenario 2, $\beta_{sim} > \beta_{jne}$ and $\beta_{jtu} > \beta_{jne}$ even though the level of
356 replacements equals the level of losses at each time step. The performance of β_{jtu} and β_{jne} is
357 even worse in scenario 3. In this case, a clear process of local extinction (species

358 replacement < species loss) would be regarded by Baselga's framework as a process of
359 replacement ($\beta_{sim} > \beta_{jne}$ and $\beta_{jtu} > \beta_{jne}$). Moreover, when the last common species disappears,
360 in spite of richness differences, there is no longer dissimilarity due to loss of species at all
361 ($\beta_{nes} = 0$ and $\beta_{jtu} = 0$) and suddenly disimilarity is entirely due to species replacement ($\beta_{sim} = 1$
362 and $\beta_{jtu} = 1$). Therefore, we argue that in this case β_{nes} and β_{jtu} are consistent with the notion
363 that two communities with no shared species could not be nested, but does not reflect the
364 process (species loss) that originated this pattern. Contrary to β_{nes} and β_{jtu}, β_{rich} is proportional
365 to the loss of species and reflects all richness differences, independently, of sites being
366 nested or not (Fig. 4, scenario 3). In conclusion, only the performance of the partitioning of β_{cc}
367 into β_{-3} and β_{rich} was consistent with the modelled gradients in all the three scenarios.
368
369 *A case study*
370 The islands of the Azorean archipelago suffered dramatic land-use changes since human
371 occupation around 600 years ago (Triantis et al. 2010). Before human settlement, Azorean
372 islands were mostly forested, but nowadays are dominated by highly modified habitats such
373 as exotic forests, semi-natural and intensive pastures, agricultural fields and orchards. Land-
374 use change has influenced all taxonomic groups, in particular the arthropods, which are the
375 richest of all taxa in the archipelago and also include the majority of endemic species (Borges
376 et al. 2010). Moreover, their distribution is often very restricted, with many species responding
377 at a fine spatial and temporal scale to habitat change (Borges et al. 2006, Cardoso et al.
378 2007, 2010, Triantis et al. 2010). Therefore, we can observe a predictably low level of species
379 replacement and a high loss of endemic species, originating richness differences, from more
380 natural to more disturbed land-use types due to selective local extinctions (Borges et al. 2008,
381 Cardoso et al. 2009b, 2010, Fattorini et al. 2012). To test the different beta diversity
382 partitioning methods under this scenario we sampled four land-use types corresponding to a
383 gradient of increasing human induced changes in Terceira Island: native forest (dominated by
384 *Laurus-Ilex*, *Juniperus* and *Erica* type forests), exotic forest (*Cryptomeria japonica* and
385 *Eucalyptus* spp.), semi-natural pasture (located above 400 m and with the grazing
386 concentrated in the summer months) and intensively managed pasture (grazed usually all
387 year) (see Borges et al. 2008, Cardoso et al. 2009b, for details). For each land-use type, eight

388 sites were surveyed, following a standard procedure (Borges et al. 2005). Briefly, at each site
389 a 150 m long transect was used to capture epigaeic fauna by pitfall trapping (30 traps
390 distributed at 5 m intervals). The majority of arthropods (except Crustacea, Acari, Collembola,
391 Hymenoptera and Diptera) were identified to species level.
392 The number of endemic species caught per sampling site decreases from native forest (mean
393 = 7.8; sd = 3.1) to intensive pastures (mean = 2.6; sd = 0.9), exotic forest (mean = 1.9; sd =
394 1.7) and semi-natural pastures (mean = 1.6; sd = 1.4). Therefore, an ecologically meaningful
395 partitioning of beta-diversity should reflect the selective extinction of endemic species into its
396 richness differences component (or nestedness component, *sensu* Baselga 2010). Moreover,
397 as very few endemic species mostly occur in disturbed habitats (Cardoso et al. 2009b,
398 Fattorini et al. 2012), some replacement could also be expected, even if replacement is
399 predictably lower than extinction. Four sampling sites were excluded from subsequent
400 analysis because no endemic species were captured (two transects in exotic forest and two
401 others in intensive pastures). We constructed a site x species matrix with the endemic
402 species and subjected it to beta diversity partitioning analysis using the different frameworks.
403 We used the non-parametric multivariate analysis of variance method (Anderson, 2001) to
404 test the null hypothesis of no differences of species replacement and richness differences
405 among the four land-use types. This method compares the variance between groups with the
406 variance within groups for a dissimilarity matrix by means of the sum of squared distances.
407 The F-ratio was calculated, as in a single factor ANOVA model, and its P-value was obtained
408 by 999 permutations. This procedure is implemented in the function “adonis” of the vegan
409 package (Oksanen et al. 2011) for the R environment (R Development Core Team (2011).
410 Via partitioning β_{cc} into β_{-3} and β_{rich}, as expected, we could reject the null hypothesis for
411 species replacement (measured by β_{-3}) and richness differences (measured by β_{rich}) and
412 concluded that there was a significant difference across the four land-use types for both
413 components of beta diversity. It is worth noting that R^2 for β_{rich} is higher than for β_{-3} indicating
414 that the process of species loss (originating richness differences) is more important than the
415 species replacement process (Table 2). Using the methods for partitioning β_{sor} into β_{sim} and
416 β_{nes} or β_{cc} into β_{jtu} and β_{jne} (Baselga 2012, 2012), we rejected the null hypothesis for species
417 replacement (measured by β_{sim} and β_{jtu}) but not the richness (nestedness) differences

418 (measured by β_{nes} and β_{jne}) caused by the loss of species (Table 2). Therefore, we concluded
419 that these frameworks failed to detect the local extinction process suffered by endemic
420 species as a consequence of land-use changes. Thus, we argue that such frameworks may
421 lead to wrong conclusions of conservation importance and land-use management strategies.
422
423
424 **Discussion**
425
426 A beta diversity partitioning method, in order to be ecologically meaningful, should reflect the
427 processes that originate community variation, species replacement and species loss (or gain)
428 and should reflect the proportional relationship between these two components (Williams,
429 1996, Williams et al. 1999, Carvalho et al. 2012). In this paper, we addressed if the behaviour
430 of three competing methods of beta diversity partitioning was consistent with these
431 expectations.
432 Comparison of the three frameworks on theoretical grounds revealed three major, closely
433 related problems in Baselga's (2010, 2012) methods. Most crucial is scaling, because the
434 species replacement fractions (β_{sim} and β_{jtu}) are not standardized the same way as the overall
435 dissimilarity measures (β_{sor} and β_{cc}, respectively) from which they are subtracted. In fact, the
436 choice of the maximum possible values for such scaling is not substantiated because there
437 are several other, equally if not more acceptable possibilities. The "replacement" fraction of
438 dissimilarity is ill-defined anyway for both cases because in the absence of nestedness beta
439 diversity is not necessarily identical to replacement. In fact, β_{sim} does not represent the
440 dissimilarity component of β_{sor} due to replacement, but represents the degree to which the
441 species-poorer sampling unit is not nested within the species-richer sampling unit (Tuomisto
442 2010).
443 As a consequence, when tested against modelled gradients, the partitioning methods
444 proposed by Baselga (2010, 2012) failed to accurately represent the species replacement and
445 species loss processes that generate community variation. Moreover, when beta diversity
446 was dominated by species losses, the measures of replacement (β_{sim} and β_{jtu}) were much
447 higher than the measures of nestedness (β_{nes} and β_{jne}, deemed to represent the loss of

448 species). Therefore, it is now clear that these methods are inappropriate to infer the relative
449 strengths of species replacement and species loss on the origins of community variation. We
450 advocate that these methods could lead to irreversible conservation and management
451 mistakes, for example, by erroneously identifying a particular area as a high replacement
452 zone where in fact the process that is occurring is selective extinction, as in the case study
453 presented in this paper.
454 To the contrary, the partition of β_{cc} into β_{-3} and β_{rich} consistently reflects the replacement and
455 species loss (or gain) processes in generating beta diversity patterns, and showed a good
456 proportional relationship between the two components when evaluated using model
457 communities. Moreover, this framework clearly identified a pattern of endemic species loss
458 associated to land-use changes in Terceira Island (Azores, Portugal). By decomposing beta
459 diversity into its two sources of variation (species replacement and species richness
460 differences) we demonstrated that community change was primarily determined by the loss of
461 endemic species (originating richness differences among sites) from natural forests to exotic
462 forests and semi-natural and intensive pastures. Before human settlement, forests occupied
463 the entire island, therefore, the loss of endemic species seems to be caused by selective
464 extinction as a consequence of species (in)tolerance to disturbance and land-use change
465 (Borges et al. 2008; Cardoso et al. 2009b, 2010).
466 In conclusion, we advocate that any beta diversity measure should be evaluated by small
467 artificial examples, simulated assemblages with well-defined properties and well-known
468 empirical gradients in order to test whether its behaviour is consistent with the process that is
469 supposed to be reflected. In the present case, we recommend the theoretically sound and
470 algebraically correct decomposition of the Jaccard index, β_{cc} into β_{-3} and β_{rich}, when the
471 objective of the study is to evaluate the relative roles of replacement and species loss (or
472 gain) in generating beta diversity patterns. Baselga's approaches may appear interesting and
473 attractive at first sight, but the methodological framework he uses is incoherent, his reasoning
474 is often self-contradictory and therefore his procedures should be applied with much care.
475
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482 - the 2010 Target" (Ref: DRCT M.2.1.2/I/003/2008).

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485 **References**

486 Almeida-Neto, M. et al. 2008. A consistent metric for nestedness analysis in ecological
487 systems: reconciling concept and measurement. – Oikos 117: 1227–1239.
488 Almeida-Neto, M. et al. 2012. Rethinking the relationship between nestedness and beta
489 diversity: a comment on Baselga (2010). – Global Ecol. Biogeogr., 21: 772-777.
490 Anderson M. J. 2001. A new method for non-parametric multivariate analysis of variance. –
491 Austral. Ecol. 26: 32-46.
492 Anderson M. J. et al. 2011. Navigating the multiple meanings of β diversity: a roadmap for the
493 practicing ecologist. – Ecol. Lett. 14: 19-28.
494 Atmar, W. and Patterson, B. D. 1993. The measure of order and disorder in the distribution of
495 species in fragmented habitat. – Oecologia 96: 373–382.
496 Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. –
497 Global Ecol. Biogeogr. 19**:** 134–143.
498 Baselga, A. 2012. The relationship between species replacement, dissimilarity derived from
499 nestedness and nestedness. – Global Ecol. Biogeogr.*,* online published, DOI:
500 10.1111/j.1466-8238.2011.00756.x.
501 Borges, P. A. V. et al. 2005. Ranking protected areas in the Azores using standardized
502 sampling of soil epigean arthropods. – Biodivers. Conserv. 14: 2029-2060.
503 Borges, P. A. V. et al. 2006. Invasibility and species richness of island arthropods: a general
504 model of endemic vs. exotic species. – J. Biogeogr. 33: 169-187.
505 Borges, P. A. V. et al. 2008. Insect and spider rarity in an oceanic island (Terceira, Azores):
506 true rare and pseudo-rare species. – In: Fattorini, S. (ed.) Insect Ecology and
507 Conservation. Research Signpost, Kerala, India, pp. 47-70.
508 Borges, P. A. V. et al. 2010. A list of the terrestrial and marine biota from the Azores. –
509 Príncipa Editora.
510 Cardoso, P. et al. 2007. Biotic integrity of the arthropod communities in the natural forests of
511 Azores. – Biodivers. Conserv. 16: 2883-2901.
512 Cardoso, P. et al. 2009a. Testing the performance of beta diversity measures based on
513 incidence data: the robustness to undersampling. – Divers. Distrib. 15: 1081-1090.
514 Cardoso, P. et al. 2009b. A spatial scale assessment of habitat effects on arthropod
515 communities of an oceanic island. – Acta Oecol. 35: 590-597.

516 Cardoso, P. et al. 2010. Drivers of diversity in Macaronesian spiders and the role of species
517 extinctions. – J. Biogeogr. 37: 1034-1046.
518 Carvalho, J. C. et al. 2012. Determining the relative roles of species replacement and
519 species richness differences in generating beta-diversity patterns. – Global Ecol.
520 Biogeogr., 21: 760-771.
521 Colwell, R. K. and Coddington, J. A. 1994. Estimating terrestrial biodiversity through
522 extrapolation. – Philos. Trans. R. Soc. (Series B) 345: 101–118.
523 Fattorini, S. et al. 2012. Use of arthropod rarity for area prioritisation: insights from the
524 Azorean islands. – PLoS ONE 7: e33995.
525 Gaston, K. J. and Blackburn, T. M. 2000. Pattern and process in macroecology. – Blackwell,
526 Oxford.
527 Harrison, S. et al. 1992. Beta diversity on geographic gradients in Britain. – J. Anim. Ecol. 61:
528 151–158.
529 Jaccard, P. 1912. The distribution of the flora in the alpine zone. – New Phytol. 11: 37-50.
530 Koleff, P. et al. 2003. Measuring beta diversity for presence-absence data. – J. Anim. Ecol.
531 72: 367–382.
532 Lennon, J. J. et al. 2001. The geographical structure of British bird distributions: diversity,
533 spatial turnover and scale. – J. Anim. Ecol. 70: 966–979.
534 Magurran, A. E. 2011. Measuring biological diversity in time (and space). – In: Magurran, A.
535 E. and McGill, B. J. (ed.) Biological diversity: frontiers in measurement and
536 assessment. Oxford University Press, pp. 85-94.
537 Melo, A. S. et al. 2009. Environmental drivers of beta diversity patterns in New-World birds
538 and mammals. – Ecography 32: 226-236.
539 Oksanen, J. et al. 2011. vegan: Community Ecology Package. R package version 2.0-2.
540 http://CRAN.R-project.org/package=vegan
541 Podani, J. & Schmera, D. 2011. A new conceptual and methodological framework for
542 exploring and explaining pattern in presence-absence data. – Oikos 120: 1625–1638.
543 Podani, J. & Schmera, D. 2012. A comparative evaluation of pairwise nestedness measures.
544 – Ecography, online published, doi: 10.1111/j.1600-0587.2011.07319.x
545 R Development Core Team 2011. R: A language and environment for statistical computing. R
546 Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL
547 http://www.R-project.org/.
548 Schmera, D. & Podani, J. 2011. Comments on separating components of beta diversity. –
549 Community Ecol. 12**:** 153–160.
550 Simpson, G.G. 1943. Mammals and the nature of continents. – Amer. J. Sci. 241: 1–31.
551 Sørensen, T. A. 1948. A method of establishing groups of equal amplitude in plant sociology
552 based on similarity of species content, and its application to analyses of the
553 vegetation on Danish commons. – Kongelige Danske Videnskabernes Selskabs
554 Biologiske Skrifter 5: 1–34.

555 Triantis, K. A. et al. 2010. The Macaronesian province: patterns of species richness and
556 endemism of arthropods. – In: Serrano, A. R. M. (ed.) Terrestrial arthropods of
557 Macaronesia – biodiversity, ecology and evolution. Sociedade Portuguesa de
558 Entomologia, Lisbon, pp. 49–71.
559 Tuomisto, H. 2010. A diversity of beta diversities: straightening up a concept gone awry. Part
560 2. Quantifying beta diversity and related phenomena. – Ecography 33: 23-45.
561 Ulrich, W. et al. 2009. A consumer's guide to nestedness analysis. – Oikos 118: 3–17.
562 Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. – Ecol.
563 Monogr. 30: 280–338.
564 Williams, P. H. 1996. Mapping variations in the strength and breadth of biogeographic
565 transition zones using species turnover. – Proc. R. Soc. B: Biological Sciences 263:
566 579–588.
567 Williams, P. H. et al. 1999. Interpreting biogeographical boundaries among Afro-tropical birds:
568 spatial patterns in richness gradients and species replacement. - J. Biogeogr. 26:
569 459–474.
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573 Supplementary material (Appendix o20980 at <www.oikosoffice.lu.se/appendix>). Appendix
574 1.
575

576 **Table 1.** Measures used in the different partitioning frameworks in which *a* is the number of
577 shared species between two sites, *b* and *c* are the numbers of exclusive species of either site
578 (Koleff *et al.* 2003).
579

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

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

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

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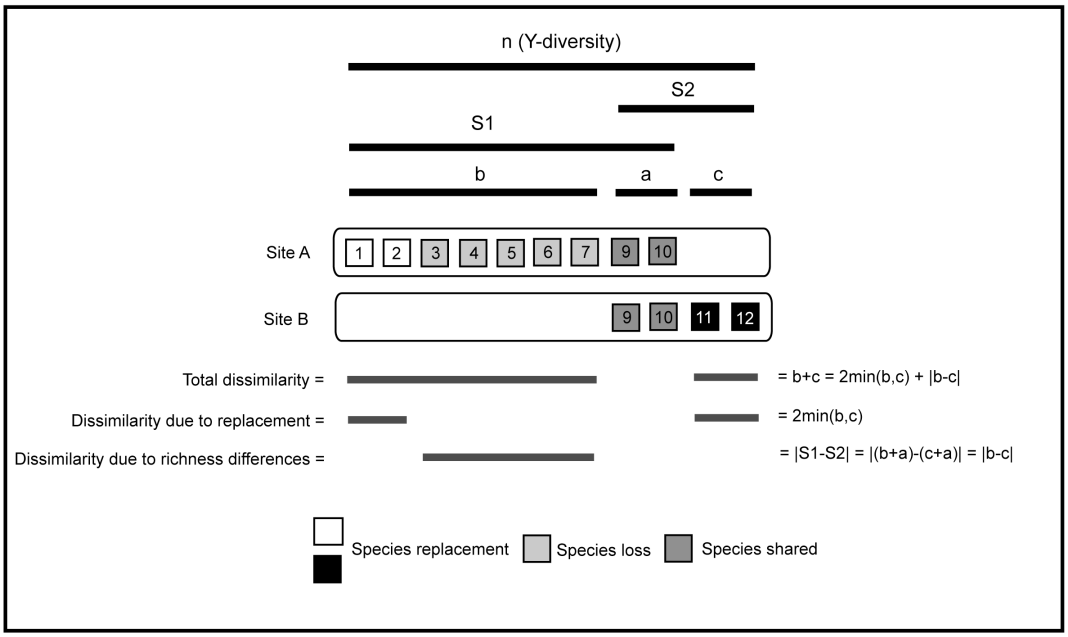

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589 **Figure 1**. Algebraic decomposition of beta diversity (total dissimilarity = b+c) of a pairwise
590 system into two additive components, species replacement (2min(b,c)) plus richness
591 difference (|b-c|). These quantities can be scaled in two different ways: i) in relation to the
592 number of species in the system (*n*), which is theoretically linked to the notion of gamma (γ)
593 diversity, ii) to the sum of species of both sites (S1 + S2). In the present example, richness
594 differences, resulting from the loss of 6 species from site A to site B, contributed more to the
595 total dissimilarity than replacement (4 species). However, β_{sim} (0.50) > β_{nes} (0.21) and β_{jtu}
596 (0.67) > β_{jne} (0.17), contrary to β_{-3} (0.33) < β_{rich} (0.5).

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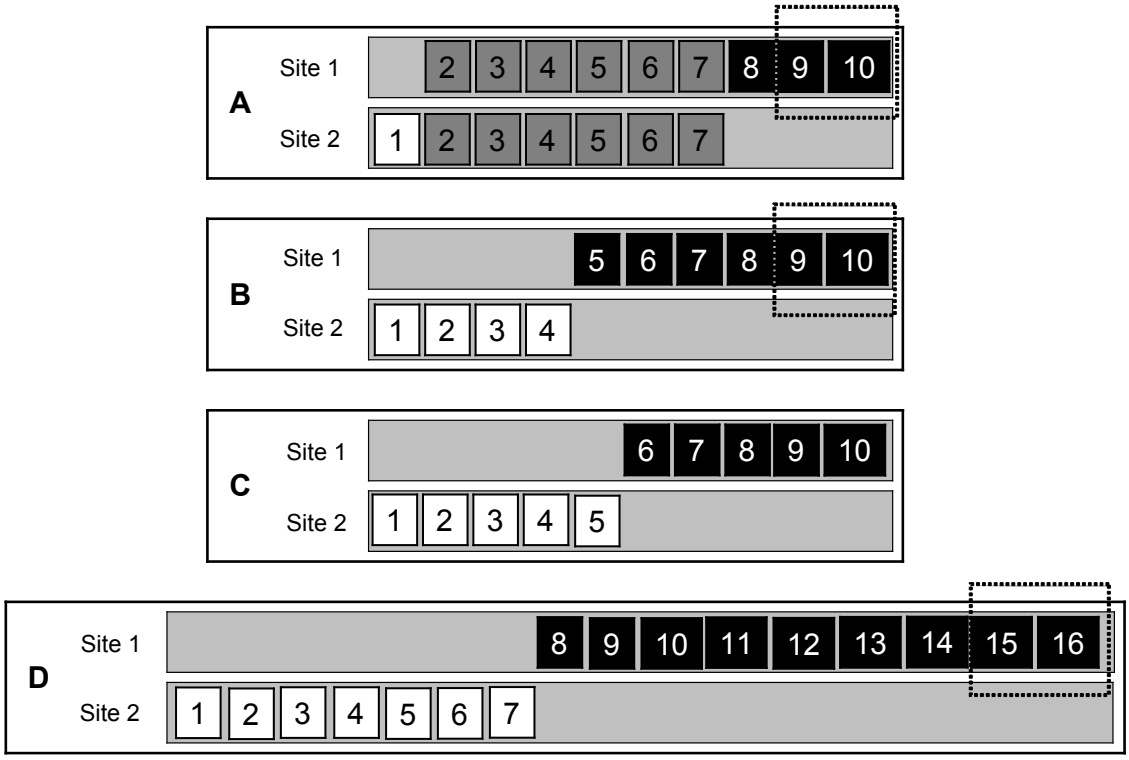
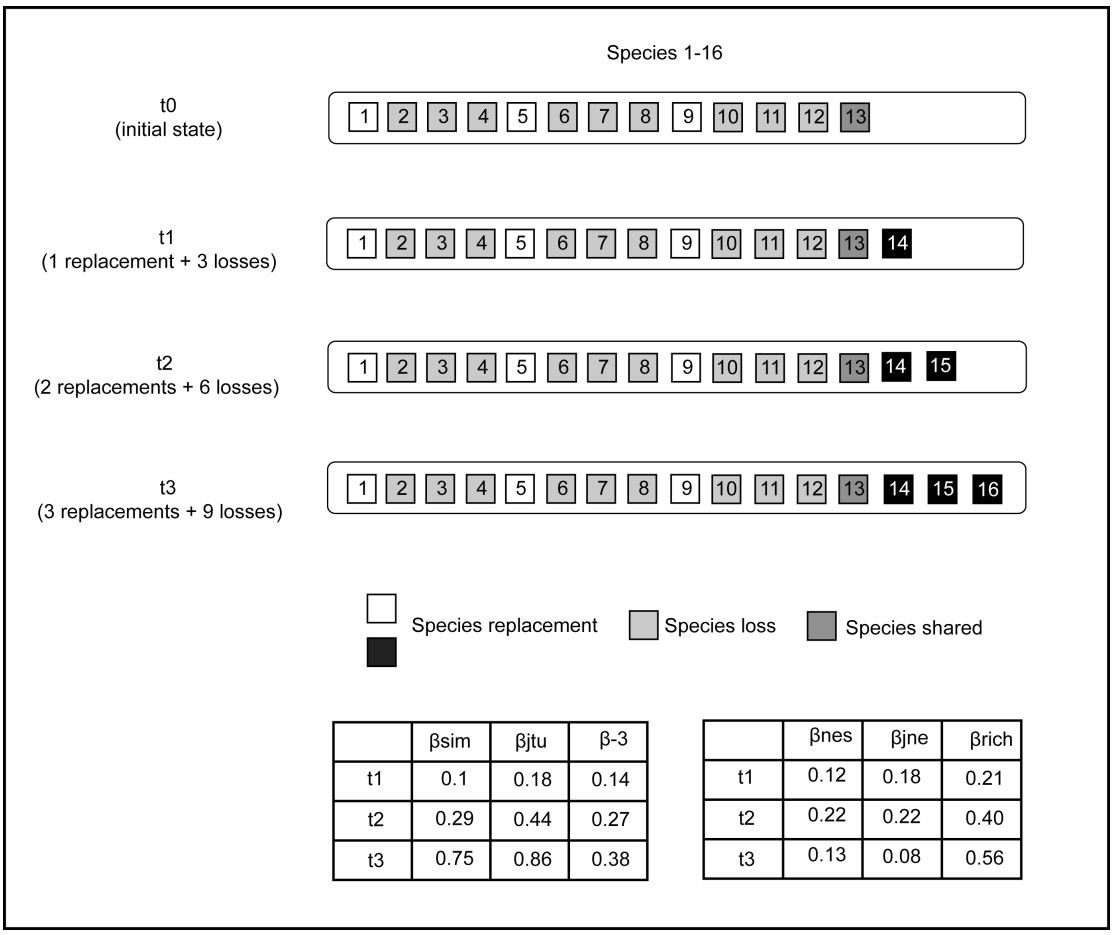


Figure 2. Comparison of possibilities for determining the theoretical upper limit of species replacement for a pair of sites (**A**) in which absolute species replacement is 2, the number of species shared is 6, and richness difference is 2. If the total number of species is kept constant, then the number of shared species may be divided equally, i.e., species 2-4 go to site 2, species 5-7 go to site 1, thus giving a value of 8 (**B**). The second possibility is splitting the set of shared species to compensate for richness differences, i.e., species 2-5 go to site 2 and species 6-7 go to site 1, yielding 10 (**C**). We may also assume that site totals remain fixed, so that the total number of species raises to 16, yielding a maximum replacement value of 14 (**D**). Black: species unique to site 1, white: species unique to site 2, dark gray: shared species. Dotted boxes enclose species responsible for richness difference.



	βsim	βjtu	β-3
t1	0.1	0.18	0.14
t2	0.29	0.44	0.27
t3	0.75	0.86	0.38

	βnes	βjne	βrich
t1	0.12	0.18	0.21
t2	0.22	0.22	0.40
t3	0.13	0.08	0.56

Figure 3. Simulation of a process of local extinctions in one site through time. Measures of dissimilarity were calculated for three time steps (t1, t2 and t3) in comparison with an initial state (t0). At each time step, one replacement (two species involved) and three losses occurred, totalling three replacements and 9 losses at the final stage (t3). Note that $\beta_{sim} > \beta_{nes}$ and $\beta_{jtu} > \beta_{jne}$, while $\beta_{-3} < \beta_{rich}$, when the loss of species is maximum and only three replacements had occurred (t3) and the humped-shaped response of β_{nes} and β_{jne} to the loss of species.

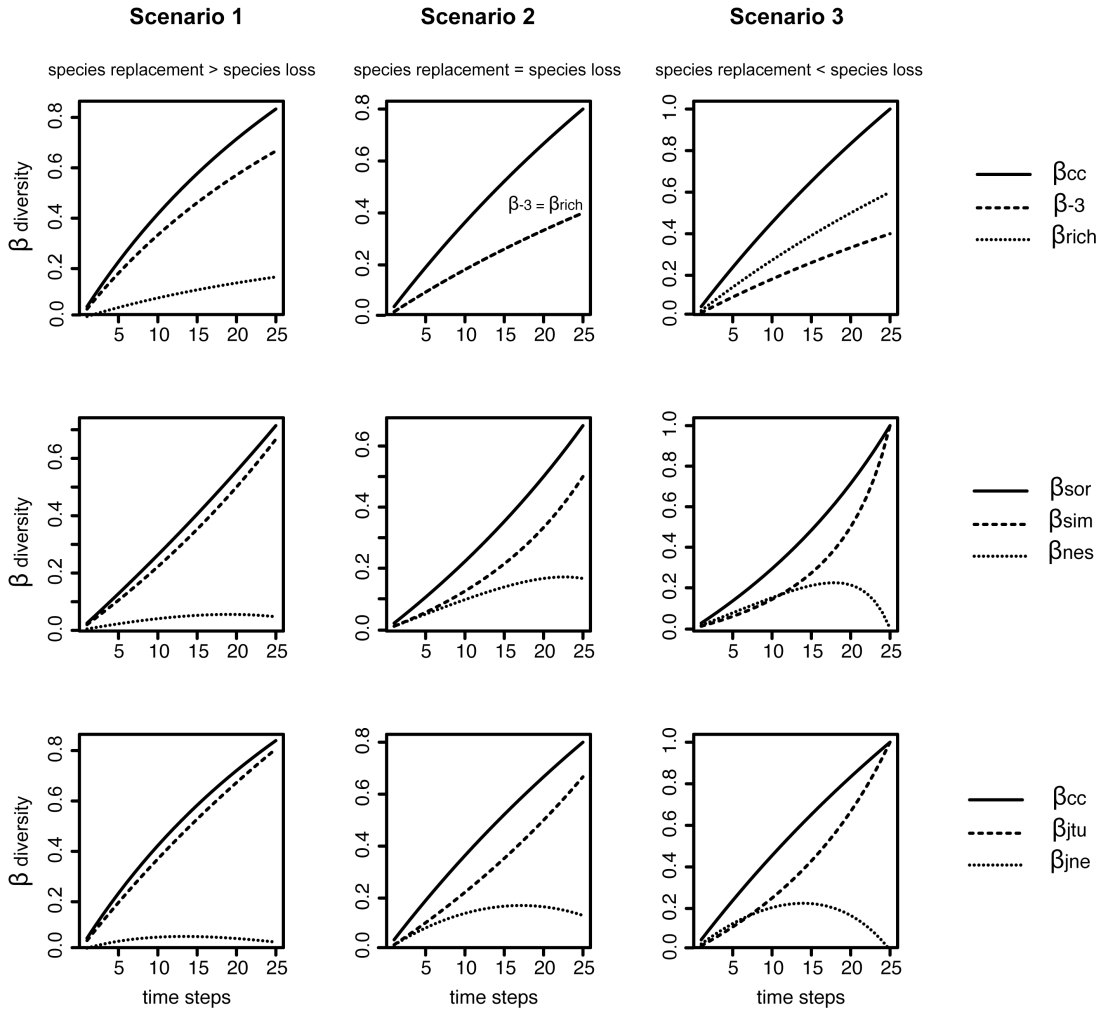


Figure 4. Response of β_{sim}, β_{nes}, β_{jtu}, β_{jne}, β_{-3}, β_{rich} in three simulated scenarios of increasing levels of species replacement and species loss along 25 time steps. In scenario 1, the number of replacements and the number of losses were set to one at each step, since one replacement involves two species, then species replacement > species loss. In scenario 2, the number of replacements was set to one, while the number of losses was set to two at each step, hence species replacement = species loss. For scenario 3, the number of replacements was set to one and the number of losses was set to three at each step, thus species replacement < species loss.