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3 **Measuring fractions of beta diversity and their relationships to**

4 **nestedness: a theoretical and empirical comparison of novel**

5 **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 β_{cc} = β_{-3} + β_{rich}, since its components are scaled in the same units and their responses are proportional to the replacement and the gain/loss of species.

Introduction

Beta diversity has been interpreted mostly as the extent of change in community composition (Whittaker 1960, Koleff et al. 2003) along a given gradient and may also be understood as variation among sampling units without any specific reference to gradients (Anderson et al. 2011). In any case, beta diversity patterns are originated from two distinct processes, the replacement and the loss (or gain) of species. Of the two, only the loss (or gain) of species causes richness differences from site to site. When losses or gains occur in a more or less ordered manner, community pattern becomes nested (Atmar and Patterson, 1993). In general, nestedness refers to the extent to which species of a smaller assemblage are a subset of a larger assemblage and is therefore a particular case of richness differences (Almeida-Neto et al. 2008, Ulrich et al. 2009). In nature, the replacement and loss (or gain) of species are combined in an infinite number of ways, leading to complex patterns of community dissimilarity. Therefore, to understand the origins of beta diversity, nestedness and their causes, one has to determine the relative roles of replacement and richness differences.

The necessity of decomposing measures of beta diversity and nestedness into comparable fractions is thus obvious. Indeed, the idea of partitioning beta diversity into different components is not new. Several authors have used various measures with different properties in order to differentiate the influence of replacement and species loss on the origins of beta diversity (Harrison et al. 1992, Williams 1996, Lennon et al. 2001, Melo et al. 2009). Nevertheless, none of these contributions established a comprehensive and unified framework for partitioning beta diversity. Recently, several attempts have been made to bridge this gap. The first one is due to Baselga (2010) proposed a general framework for unifying the different components of beta, suggesting partitioning pairwise beta diversity expressed by the Sørensen dissimilarity into replacement (turnover) and "nestedness resultant" components. An alternative solution has also been proposed independently by Podani and Schmera (2011) and Carvalho et al. (2012). In this, beta diversity is measured by Jaccard dissimilarity which is decomposed into replacement and richness difference fractions. The richness difference fraction is taken as a positive contributor to a nestedness measure

86   suggested by Podani and Schmera (2011). Even more recently, Baselga (2012) has rejected

87   this suggestion and proposed decomposing Jaccard dissimilarity in the same fashion as the

88   Sørensen index. Unfortunately, these different methods can lead to radically different

89   conclusions about the same dataset (Carvalho et al. 2012) making inevitable the comparison

90   of these approaches so that users of either approach can learn their relative merits and

91   potential pitfalls and limitations.

92   In this paper, we argue that any partitioning of beta diversity should reflect properly the

93   replacement and the loss (or gain) of species in order to be useful and ecologically

94   meaningful. We review the concepts behind the different frameworks and the consistency of

95   their performance with this expectation. For simplicity, we will focus only on pairwise

96   comparisons of assemblages, although the conclusions could be extended to multiple-

97   assemblage comparisons. First, we shall use arithmetic equations and small artificial

98   examples to provide well defendable mathematical support for our arguments and to allow the

99   reader to interpret the performance of the competing numerical approaches in a clear way.

100 Then, our arguments are supported further by simulated examples and an actual case study

101 on changes of the endemic arthropod fauna of Terceira Island (Azores, Portugal).

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103 **Existing methods for partitioning beta diversity**

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105 To save space, an overview of abbreviations and the mathematical formalism is summarized

106 in tabular form (Table 1). Note that replacement and (species) turnover are regarded as

107 synonyms. The method proposed by Baselga (2010) consists in partitioning pairwise

108 Sørensen dissimilarity (β_{sor}) into two components: dissimilarity due to species replacement

109 (β_{sim}) plus dissimilarity due to nestedness (β_{nes}),

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111 $\beta_{sor} = \beta_{sim} + \beta_{nes}$.

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113 The rationale of this method is based on the fact that β_{sor} is sensitive to replacement and

114 richness differences and β_{sim} (well-known as Simpson dissimilarity) seems to be sensitive to

115 replacement only. Because, in the absence of nestedness, $\beta_{sor} = \beta_{sim}$, Baselga deduced that

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

117   The performance of Baselga's (2010) method was found to be inconsistent with the variation

118   of species replacement and species loss (Podani and Schmera 2011, Schmera and Podani

119   2011, Almeida-Neto et al. 2012, Carvalho et al. 2012). A new partitioning of beta diversity, due

120   to Podani and Schmera (2011) and Carvalho et al. (2012) provides formal definitions of both

121   absolute and relativized measures in terms of the parameters of the 2x2 contingency table

122   (Table 1). Absolute beta diversity is expressed as b+c (Weiher - Boylen beta, see Koleff et al.

123   2003), which is divided into species replacement and richness difference fractions. The term

124   replacement means that a species in one site is substituted by a species in another site (or

125   point of time in the same site). Therefore, one replacement always involves two species and

126   the total number of replaced species is equal to 2min(b,c). Richness differences arise from

127   the loss (or gain) of species and are measured as |b-c|. Therefore, the contingency table can

128   be algebraically decomposed into two biologically sound asymmetric components, according

129   to the expression:

130

131   b+c = 2min(b,c) + |b-c|

132

133   (Fig. 1). Under this framework, nestedness is conceived, in absolute terms, as the sum of two

134   independent components, overlap (a) and richness difference (|b–c|) with the condition a>0

135   (Podani and Schmera 2011, 2012).

136   Relativization of beta diversity may be achieved by division with the total number of species of

137   the system (n=a+b+c), which has an obvious theoretical link to the gamma diversity concept

138   as applied to pairs of sites. Thus, we have the Jaccard dissimilarity β_{cc} (β_{jac} in Baselga'

139   notation) which can be decomposed into relativized species replacement or dissimilarity due

140   to replacement ($\beta_{-3,}$ or R_{rel} in Podani and Schmera's notation) and relativized richness

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

142

143   β_{cc} = β_{-3} + β_{rich}.

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145   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}

176 and β_{cc} are not mathematically and conceptually equivalent to the replacement given by β_{sim}

177 and β_{jtu}, respectively.

178 The scaling problem has been illuminated numerically by small artificial examples in Schmera

179 and Podani (2011). Nevertheless, in order to have a complete picture on the subject matter in

180 this communication as well, we provide another convincing example. Suppose that a = 3, b =

181 5 and c = 2. From these values we obtain that β_{sor} = 7/13, β_{sim} = 2/5 and β_{nes} = 9/65 (since

182 7/13–2/5 = 3/13 · 3/5 = 9/65). While β_{sor} expresses the proportion of total presence scores

183 (i.e., 2a+b+c = 13) that are not shared by the two sites, β_{sim} corresponds to the proportion of

184 presence scores in the poorer site (a + min(b,c) = 5) which are not present in the other site.

185 The value of 9/65, however, does not reflect any reasonable quantity in terms of species

186 numbers and their proportions. The reason is that Sørensen dissimilarity and Simpson

187 dissimilarity are differently scaled (to 13 versus 5), notwithstanding that they have the same

188 range (0 to 1). Subtracting a quantity from another is indeed incorrect logically if the

189 measurement units or the scale of the two are not identical. We may thus conclude that

190 Simpson dissimilarity is an unjustified choice for measuring replacement, if beta diversity is

191 expressed by Sørensen dissimilarity.

192 The decomposition of β_{cc} as suggested by Baselga (2012) suffers from the same drawback as

193 that of β_{sor}: different scaling and therefore lack of common currency. Using the same example

194 as above, β_{jne} = β_{cc} − β_{jtu} = 7/10 − 4/7 = 9/70. Similarly to the previous case, we are unable to

195 attribute any meaning to this result, so that any suggestion as to the direct ecological

196 interpretation of this value in terms of absolute species numbers or their proportions would be

197 warmly welcome. β_{jtu} is apparently a less fortunate choice for quantifying species replacement

198 if beta diversity is expressed by the Jaccard index.

199 By contrast, our approach offers easy interpretation of results both *mathematically* and

200 *ecologically.* For the same example as above, the meaning of absolute values is

201 straightforward: b+c=7 is the number of species not shared by the two sites (beta),

202 2min{b,c}=4 is species replacement and |b–c| = 3 is richness difference. By standardization

203 with n (=10), we obtain the Jaccard index, β_{cc} = 7/10, relativized species replacement, β_{-3} =

204 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 $a+2\min(b,c)$

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 $2\min(b,c)/(a+2\min(b,c))$ 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 $a+2\min(b,c)$ 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 $a + 2\min(b,c)$.

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

234   circumstances can a+2min(b,c) be the maximum. Assume first that the total number of

235   species in the two sites is constant, so the theoretical maximum can only be determined

236   by breaking up joint presences in the data. The use of a+2min(b,c) as denominator

237   implies that maximum is reached when a/2 species remain only in site 1 and a/2

238   species in the other (Fig. 2.A and B). Complications may arise, of course, when "a" is

239   an odd number. Nonetheless, the two sites can be "potentially" equally rich and

240   replacement even higher if the set of shared species is split between the sites such that

241   their richness difference is compensated for (Fig. 2.A and C). The extent to which this

242   compensation is possible is determined by |b–c|, so that the maximum of species

243   replacement can be higher than a+2min(b,c) and is in fact constrained by both sites

244   whenever |b–c|>0. We can imagine another reasonable solution in which the number of

245   species in each site remains constant and the total number of species increases. As

246   seen in Fig. 2.D, in this case the maximum is 2a+2min{b,c}, larger than what Baselga

247   (2012) proposed.

248   • However, when interest lies in the replacement component of Jaccard dissimilarity, then

249   there is no reason to consider at all what the maximum of replacement can be; interest

250   is merely focused on the absolute or relative contribution of the subset of species that

251   are actually responsible for replacement. For this purpose, the use of "n" (gamma

252   diversity) as the denominator is the correct and, in fact, the only meaningful choice. We

253   disagree with the proposal, therefore, that the rationale behind measures of species

254   replacement "dictates" (as stated in Baselga 2012) the choice of the denominator as the

255   number of species that could potentially be replaced.

256   • The proposed replacement formula 2min(b,c)/(a+2min(b,c)) does not satisfy the

257   requirements set up by Baselga (2012, p. 3, right column in the Early View document)

258   himself, namely, that "adding unique species to only one of the sites should not affect

259   the replacement measure". If a new species is added to the species poorer site, then

260   the replacement measure suggested by Baselga (2012) does change. (For example, for

261   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

262   of this new species clearly modifies the nominator and the denominator, thus the

263   *proportion* of the species shared as well, so that the above requirement is in clear

264   conflict with the following one "any change in the proportion of species shared between

265   two sites should be reflected by a meaningful measure of species replacement"

266   (Baselga 2012, p. 3, right column in the Early View document). It was specified by

267   Baselga (2012) as the second main property that a meaningful replacement function

268   must have. Confusion around admissible properties of the replacement index probably

269   came from the fact that in Fig. 1 of Baselga (2012) changes are monitored over

270   increases of n, while n remains constant in his Fig. 2.

271 In conclusion, measurement of replacement separately and measurement of the contribution

272 of replacement to some other measure in Baselga's (2010, 2012) proposals are contradicting

273 and, even if a separate coefficient is sought, the proposed formula does not satisfy the

274 requirements set up by its own proponent.

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276 *Decomposition of beta diversity in the absence of nestedness*

277 Now we examine the deduction that in absence of nestedness, i.e., when the nestedness

278 resultant component is zero (a = 0), both total beta diversity and its replacement component

279 take the value of 1, no matter whether Sørensen or Jaccard dissimilarity is partitioned.

280 Baselga (2010, 2012) overlooked the fact that beta diversity is not always identical to species

281 replacement if nestedness is lacking. We demonstrate this by the following three examples for

282 site pairs j and k:

283   **a**   **b**   **c**

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

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294 In all cases, $\beta_{sor} = \beta_{sim} = 1$ as well as $\beta_{cc} = \beta_{jtu} = 1$. However, in absolute terms beta diversity is

295 dominated by richness difference in **a** (1 species replaced by another but k has six other

296 species), richness difference and species replacement are more balanced in **b** (3 species are

297 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).

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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.

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423

424   **Discussion**

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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.

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573   Supplementary material (Appendix o20980 at <www.oikosoffice.lu.se/appendix>). Appendix
574   1.

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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).

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

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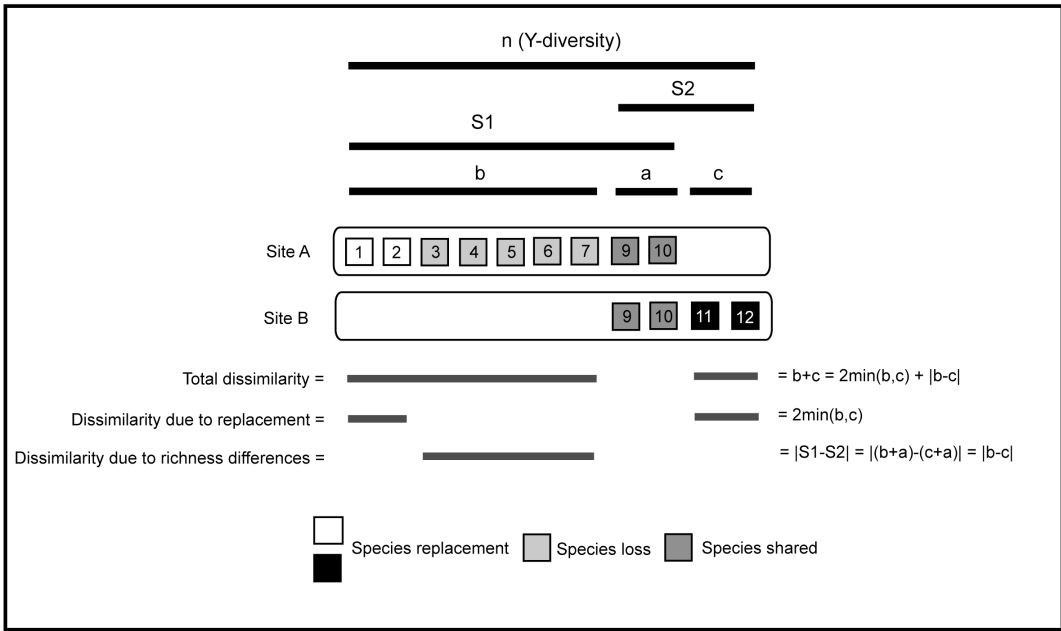
Figure 1. Algebraic decomposition of beta diversity (total dissimilarity = b+c) of a pairwise system into two additive components, species replacement (2min(b,c)) plus richness difference (|b-c|). These quantities can be scaled in two different ways: i) in relation to the number of species in the system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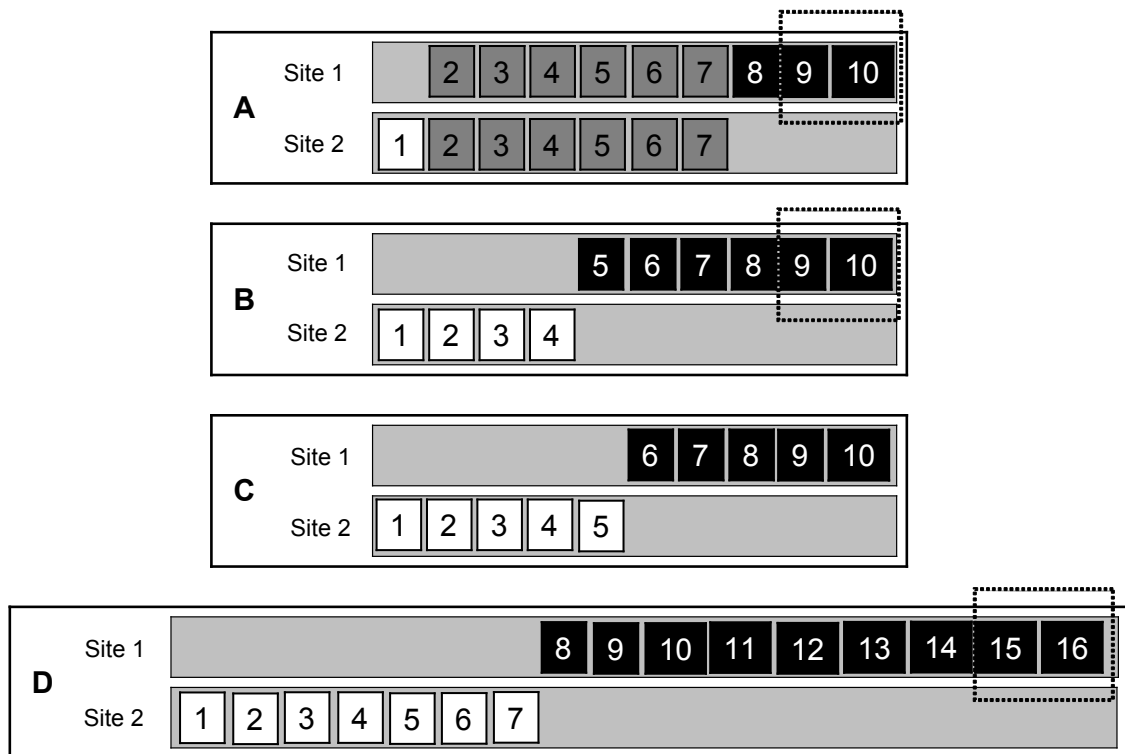
Figure 2. Comparison of possibilities for determining the theoretical upper limit of species replacement for a pair of sites (**A**) in which absolute species replacement is 2, the number of species shared is 6, and richness difference is 2. If the total number of species is kept constant, then the number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

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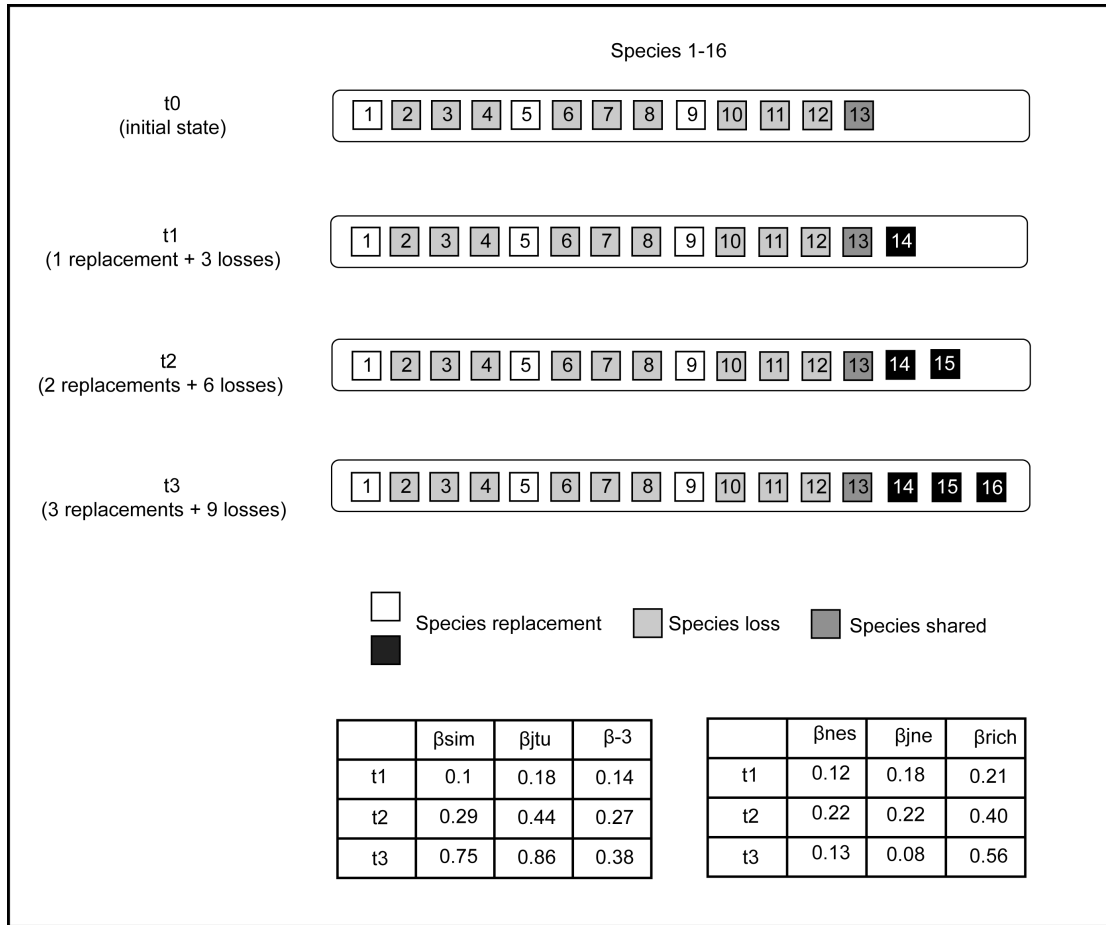
Figure 3. Simulation of a process of local extinctions in one site through time. Measures of dissimilarity were calculated for three time steps (t1, t2 and t3) in comparison with an initial state (t0). At each time step, one replacement (two species involved) and three losses occurred, totalling three 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.

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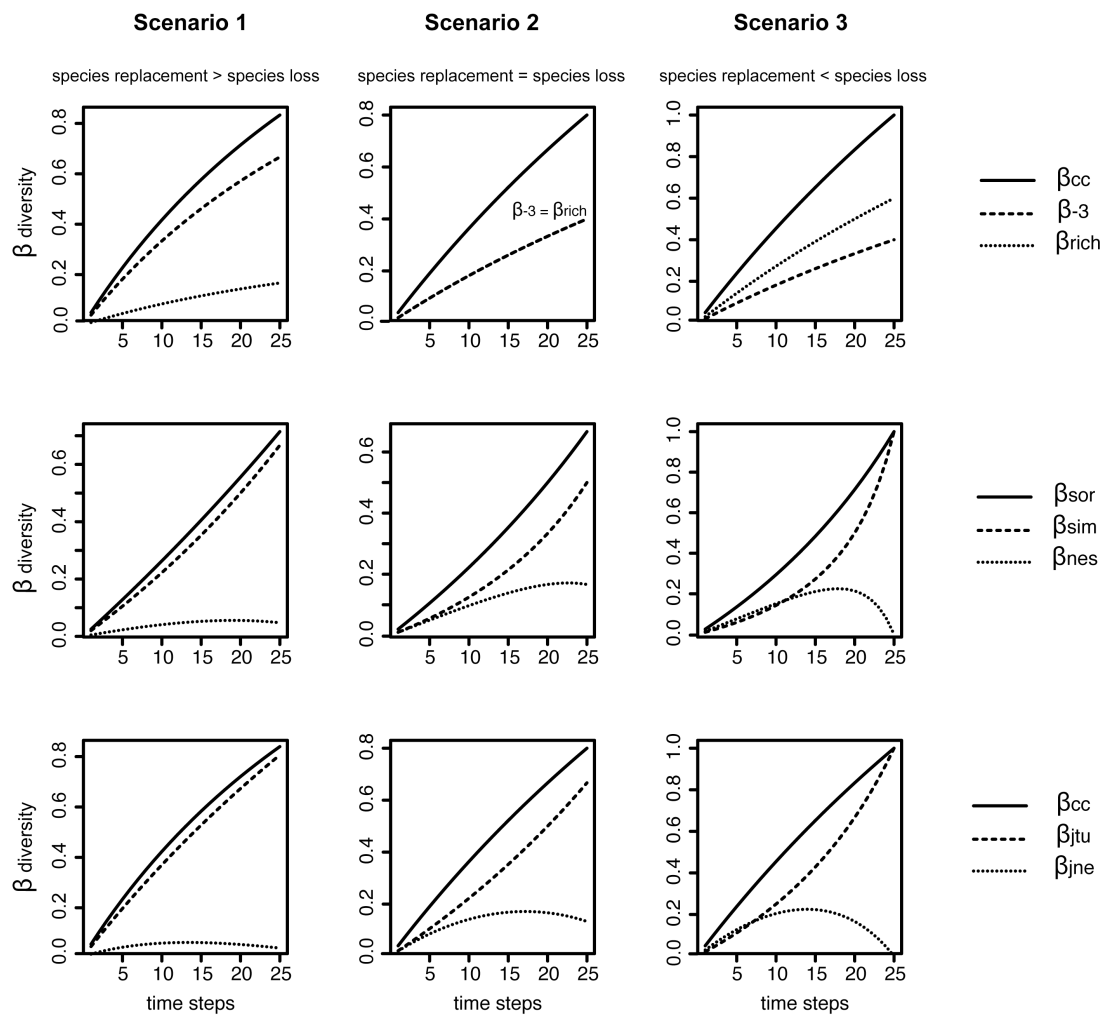
Figure 4. Response of β_{sim}, β_{nes}, β_{jtu}, β_{jne}, β_{-3}, β_{rich} in three simulated scenarios of increasing levels of species replacement and species loss along 25 time steps. In scenario 1, the number of replacements and the number of losses were set to one at each step, since one replacement 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.

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