

Research article

Partitioning the temporal changes in abundance-based beta diversity into loss and gain components

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Running headline: Partitioning temporal changes in beta diversity

1 **ABSTRACT**

- 2 1. Ecologists have long recognized that the losses and gains in local species abundances can
3 either decrease or increase spatial beta diversity, phenomena often referred to as biotic
4 homogenization and differentiation, respectively. However, quantifying such dynamic
5 impacts of species abundances on beta diversity has remained a methodological challenge.
- 6 2. Here, we develop a numerical method to additively partition the temporal changes in beta
7 diversity into distinct components that reflect the losses and gains in local species
8 abundances. Our method is based on Ružička and Bray–Curtis indices and the normalized
9 abundance-based Whittaker’s beta diversity. The temporal changes in these measures are
10 partitioned into components that represent biotic homogenization and differentiation driven
11 by abundance losses and gains at both species and community levels.
- 12 3. Application of the method to a Swedish fish community dataset revealed decreases in beta
13 diversity between 1990 and 2018. The homogenization of fish communities was explained
14 by gains, but not losses, in species abundances across sites. Species-level partitioning further
15 showed that the homogenization was largely caused by the increased population sizes of a
16 **particular species** in sites where it was already present.
- 17 4. The results highlight that our partitioning method effectively identifies local population and
18 community processes embedded in regional biodiversity patterns. We believe that explicit
19 analyses of the losses and gains in species abundances should bring deeper insights into the
20 dynamics of beta diversity.

21 **Keywords:** Biotic homogenization, Community assembly, Compositional dissimilarity,
22 Ecological dynamics, Metacommunity, Spatial heterogeneity, Species turnover, Time series

1 | INTRODUCTION

Beta diversity, the variation in the identities and abundances of species among sites, is a fundamental facet of biodiversity (Whittaker, 1960; Koleff et al., 2003; Anderson et al., 2011). Beta diversity can be quantified in two ways, namely by using incidence-based (i.e., presence–absence-based) and abundances-based approaches (Chao et al., 2005; Legendre & Legendre, 2012; Baselga, 2013). The two approaches weigh rare and dominant species differently and thus offer complementary insights into community structure (Anderson et al., 2011; Legendre & Legendre, 2012; Li et al., 2016). Extensions of existing methods for analyzing incidence-based beta diversity to account for abundance can bring a more comprehensive understanding of biodiversity (Baselga, 2013; Chao et al., 2014).

While the replacements of endemic species by cosmopolitan nonnative species have been a global concern (McKinney & Lockwood, 1999), we still have mixed evidence for the consequent changes in beta diversity over time (Olden et al., 2018). The temporal decreases and increases in beta diversity, referred to as biotic homogenization and differentiation, respectively, subsume complex processes of local population dynamics (McKinney & Lockwood, 1999; Olden & Poff, 2003; Socolar et al., 2016; Rosenblad & Sax, 2017; Tatsumi et al., 2020). Empirical and simulation studies have shown that incidence- and abundance-based approaches can result in contrasting signs and magnitudes of temporal changes in beta diversity (Cassey et al., 2008; Li et al., 2016; Petersen et al., 2021). To build a more rigorous evidence base for biotic homogenization and differentiation, we need a tool to disentangle the processes underlying beta diversity changes.

Species extinctions and colonizations (i.e., changes in presence–absence status) can alter beta diversity in multiple ways (Olden & Poff, 2003; Rosenblad & Sax, 2017; Tatsumi et al., 2020, 2021). Specifically, extinctions lead to biotic homogenization when rare, infrequent species become regionally extinct, but otherwise result in differentiation (Socolar et al., 2016; Rosenblad & Sax, 2017; Tatsumi et al., 2020). Colonizations cause homogenization when species new to the region become widespread or existing species increase their regional dominance, but drive differentiation when new species colonize a small number of sites (Socolar et al., 2016; Rosenblad & Sax, 2017; Tatsumi et al., 2020). **Extinctions and colonizations can also mask each other by one increasing beta diversity and the other decreasing it (Tatsumi et al., 2020, 2021).** In our previous study (Tatsumi et al., 2021), we proposed a numerical method to additively partition such impacts of extinction and colonization on spatial beta diversity as quantified by incidence-based measures, namely Jaccard and Sørensen indices and Whittaker's beta diversity.

Here, we develop a new method to additively partition the impacts of abundance losses and gains on spatial beta diversity by extending our previous incidence-based method. Similar to species extinctions and colonizations (i.e., binary changes between presence and absence), quantitative decreases and increases in local species abundances can drive either homogenization or differentiation (Socolar et al., 2016). The new method that we propose here allows one to partition such temporal changes in spatial variation ($\Delta\beta = \beta' - \beta$, where β and β' are the values at $t = 1$ and 2, respectively) into distinct terms that reflect abundance losses and gains (Figure 1). **Our method helps to resolve the local population dynamics and metacommunity processes embedded**

64 in regional biodiversity patterns using both incidence and abundance data.

65

66 2 | METHODS

67 The partitioning method described below can be implemented using the `ecopart` R package
68 available from GitHub: `remotes::install_github("communityecologist/ecopart")`.

69

70 2.1 | Partitioning equations

71 We describe the additive partitioning of temporal changes in pairwise dissimilarity measures,

72 namely using Ružička ($\beta_{Ruž}$) and Bray–Curtis indices (β_{BC}) (Bray & Curtis, 1957; Ružička,

73 1958). These measures are defined as $\beta_{Ruž} = \sum_{i=1}^S u_i / \sum_{i=1}^S (c_i + u_i)$ and $\beta_{BC} =$

74 $\sum_{i=1}^S u_i / \sum_{i=1}^S (2c_i + u_i)$, where c_i is the component of species abundance common to both sites,

75 u_i is the component of species abundance unique to either site, i is species identity, and S is the

76 number of species. Here, let $\beta^{(\lambda)} = \sum_{i=1}^S u_i / \sum_{i=1}^S (\lambda c_i + u_i)$, then $\beta_{Ruž} = \beta^{(1)}$ and $\beta_{BC} = \beta^{(2)}$.

77 Ružička and Bray–Curtis indices are abundance-based extensions of Jaccard and Sørensen

78 indices, respectively, for which the partitioning methods have already been described (Tatsumi et

79 al., 2021). **Although the Ružička and Bray–Curtis indices have different statistical properties**

80 **from other common dissimilarity measures (e.g., Shannon entropy; Jost, 2007), we use the two**

81 **indices here on account of their mathematical simplicity and wide uses in ecology.**

82 Previous studies **categorized** species extinction and colonization **into six types** based on

83 their impacts on spatial dissimilarity (Rosenblad & Sax, 2017; Tatsumi et al., 2020, 2021). We

84 here extend these definitions to account for species abundances (Figure 2). The first type is the

85 reduction in u_i (type 1 in Figure 2); that is, for the abundance of a given species i in site k (a_{ik}), a

86 component that was unique to either site (u_i) at time $t = 1$ becomes lost at time $t = 2$. Type 2 is the

87 case where a component of a_{ik} that was common to both sites (c_i) becomes lost by an equal

88 amount in both sites. Type 3 refers to the loss in c_i in the site where a_{ik} was smaller than, or equal

89 to, that in the other site, turning c_i into u_i . Type 4 refers to the gain in u_i in the site where a_{ik} was

90 larger than, or equal to, that in the other site. Type 5 is the case where c_i increases by an equal

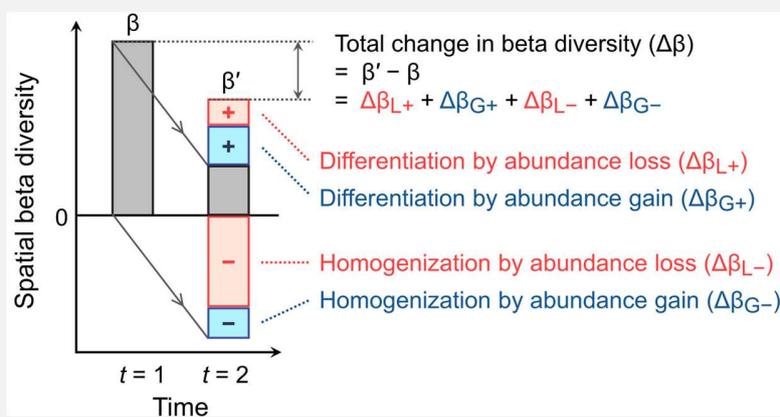


Figure 1. Temporal change in spatial beta diversity and its additive components. The components represent biotic homogenization or differentiation driven by losses or gains in species abundances.

91 amount in both sites. Type 6 refers to the gain in c_i in the site where a_{ik} was smaller than the other
 92 site, turning u_i into c_i . Types 1, 5, and 6 decrease $\beta^{(\lambda)}$, leading to homogenization, whereas types
 93 2, 3, and 4 increase $\beta^{(\lambda)}$, leading to differentiation. We write l_i^{L} , l_i^{E} , l_i^{S} , g_i^{L} , g_i^{E} , and g_i^{S} for the
 94 amount of changes in abundance that correspond to types 1, 2, 3, 4, 5, and 6, respectively
 95 (Appendix S1).

96 It is possible for the abundance of a given species i to change differently in the two sites
 97 within the same time interval. Namely, if the abundance a_{ik} decreases in one site (e.g., $k = 1$)
 98 where it was larger and increases in the other site (e.g., $k = 2$) where it was smaller, then beta
 99 diversity can potentially show no net change (see the bottom case in Figure 2). We refer to such
 100 offsetting replacements in species abundances as hidden dynamics (Tatsumi et al. 2021). We
 101 write d_i for the changes in abundance that fall under this definition. In our partitioning method,
 102 we explicitly describe d_i as a distinct form of abundance losses and gains. In total, there are 32
 103 possible ways a_{ik} can decrease and/or increase, including the hidden dynamics (Appendix S1).
 104 Further, beta diversity can be much more dynamic than any index portrays since abundances can
 105 change multiple times and in multiple ways between sampling intervals, and so here c_i and u_i
 106 refer to the net change between $t = 1$ and 2.

107 For brevity, we write the sum of a given variable across all species ($1, 2, \dots, S$) by using the
 108 uppercase letters (e.g., $\sum_{i=1}^S u_i = U$, $\sum_{i=1}^S d_i = D$, and $\sum_{i=1}^S l_i^{\text{L}} = L^{\text{L}}$). The temporal changes in C
 109 and U can then be written as $\Delta C = C' - C = -L^{\text{E}} - L^{\text{S}} + G^{\text{E}} + G^{\text{S}}$ and $\Delta U = U' - U = -L^{\text{L}} + L^{\text{S}} +$
 110 $G^{\text{L}} - G^{\text{S}}$. We can additively partition the temporal changes in pairwise dissimilarity ($\Delta\beta^{(\lambda)} =$
 111 $\beta'_{\text{Ruž}} - \beta_{\text{Ruž}}$ when $\lambda = 1$ and $\Delta\beta^{(\lambda)} = \beta'_{\text{BC}} - \beta_{\text{BC}}$ when $\lambda = 2$) into six terms that correspond to the
 112 six types of abundance changes:

$$\begin{aligned}
 113 \quad \Delta\beta^{(\lambda)} &= \beta^{(\lambda)'} - \beta^{(\lambda)} \\
 114 \quad &= \underbrace{-\frac{p}{U}(L^{\text{L}} + D)}_{\Delta\beta_1} + \underbrace{\frac{p}{C}L^{\text{E}}}_{\Delta\beta_2} + \underbrace{\left(\frac{p}{U} + \frac{p}{C}\right)L^{\text{S}}}_{\Delta\beta_3} \\
 115 \quad &+ \underbrace{\frac{p}{U}(G^{\text{L}} + D)}_{\Delta\beta_4} + \underbrace{\frac{-p}{C}G^{\text{E}}}_{\Delta\beta_5} + \underbrace{\left(-\frac{p}{U} - \frac{p}{C}\right)G^{\text{S}}}_{\Delta\beta_6} \quad (1)
 \end{aligned}$$

116 where $p = \frac{\lambda c U}{(\lambda c + U)(\lambda c' + U')}$ and C and U are both non-zero. See Appendix S1 for derivation of the
 117 equation.

118 The variable D denotes the hidden dynamics. The quantities $-\frac{p}{U}D$ in $\Delta\beta_1$ and $-\frac{p}{U}D$ in $\Delta\beta_4$
 119 cancel each other out by summing up to zero. These two quantities thus allow us, without causing
 120 any effect on $\Delta\beta$, to explicitly account for D in a manner comparable to $-\frac{p}{U}L^{\text{L}}$ and $-\frac{p}{U}G^{\text{L}}$.

121 **The first three terms are associated with gains, while the last three are associated with**
 122 **losses. The six terms respectively correspond to the six types of abundance changes described in**
 123 **Figure 2.** The first term, which is always negative, represents homogenization by abundance
 124 losses ($\Delta\beta_{\text{L-}}$). The second and third terms, which are always positive, indicate differentiation by
 125 abundance losses ($\Delta\beta_{\text{L+}}$). Similarly, the fourth term represents differentiation by abundance gains

126 ($\Delta\beta_{G+}$) and the fifth and sixth terms indicate homogenization by abundance gains ($\Delta\beta_{G-}$).
127 Depending on the ecological question at hand, one can sum the terms as $\Delta\beta_L = \Delta\beta_{L-} + \Delta\beta_{L+}$ and
128 $\Delta\beta_G = \Delta\beta_{G-} + \Delta\beta_{G+}$ to assess the total impact of abundance losses and gains on $\Delta\beta$, respectively
129 (Figure 1).

130 See [Appendix S2](#) for the responses of $\Delta\beta$ components ($\Delta\beta_{L-}$, $\Delta\beta_{L+}$, $\Delta\beta_{G-}$, and $\Delta\beta_{G+}$) to the
131 abundance losses and gains (L^L , L^E , L^S , G^L , G^E , G^S , and D).

132

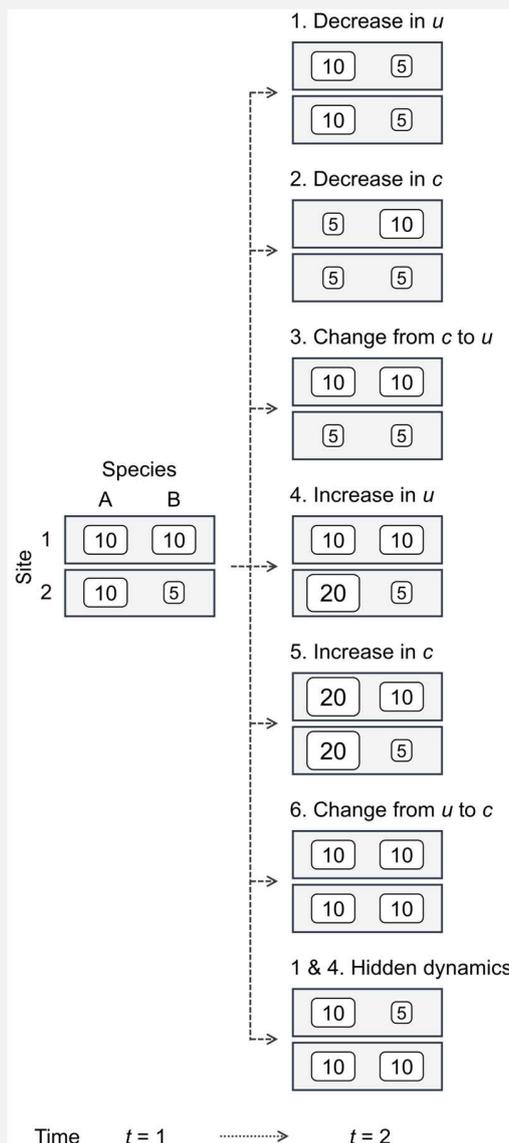


Figure 2. Schematic representation of six types of changes in beta diversity and hidden dynamics. The numbers in the boxes indicate species abundances. The variable u denotes the components of abundance unique to either site and c denotes the components of abundance common to both sites. For example, at $t = 1$, the u of species A is 0 and species B is 5. The c of species A is 10 and species B is 5. Thus, taking Ružička index as an example, $\beta_{\text{Ruž}} = (0 + 5)/(10 + 5 + 0 + 5) = 1/4$. In type 1 at $t = 2$, the u of species B becomes 0 as a result of an abundance loss in one of the two sites. Consequently, $\beta_{\text{Ruž}}$ decreases to 0. In type 2, the c of species A is reduced to 5 and thus $\beta_{\text{Ruž}} = (0 + 5)/(5 + 5 + 0 + 5) = 1/3$. We can see from these examples that, while types 1 and 2 are both associated with abundance losses, the changes in $\beta_{\text{Ruž}}$ can take either negative or positive values. It is such distinct ways of changes in beta diversity our method allows one to partition.

133 2.2 | Multisite variation

134 Our partitioning method is applicable to multisite measures of beta diversity. Multisite measures
135 are used to quantify variation among more than two sites (Baselga, 2010). Averaging pairwise
136 dissimilarities (such as β_{RuZ} or β_{BC}) across pairs of sites is a suboptimal approach due to their lack
137 of statistical independence (Baselga, 2010, 2017).

138 In Appendix S3, we demonstrate the partitioning of multisite beta diversity by taking, as an
139 example, the normalized abundance-based Whittaker's beta diversity (β_w) (cf. Baselga, 2017).
140 We chose β_w here on account of its simple mathematical structure. Note, however, that future
141 works are needed for partitioning other multisite indices, typically beta diversity based on Hill
142 numbers (see *Discussion* for detail).

144 2.3 | Species-level impacts on beta diversity

145 We can further use the partitioning equations to quantify the response of beta diversity to the
146 losses and gains in the abundance of each species independently. For example, consider a case
147 where the abundance of a species that had existed in one site was completely lost (i.e., the species
148 went locally extinct). This loss will add $-\frac{p}{U}L^L$ to $\Delta\beta$ in Eqn. 1. Thus, the added value can be
149 interpreted as the consequence of the focal species' abundance loss on beta diversity. In this way,
150 $\Delta\beta$ can be additively partitioned into components that reflect the decreases and increases in the
151 population size of individual species. Note that it is possible for the population size of a given
152 species to decrease in some sites while increase in other sites within the same time interval,
153 generating both the loss and gain components (i.e., $\Delta\beta_{L-}$, $\Delta\beta_{L+}$, $\Delta\beta_{G-}$, and $\Delta\beta_{G+}$).

155 3 | APPLICATIONS

156 We applied the partitioning method to riverine fish community data retrieved from the Swedish
157 Electrofishing Register database (Sers, 2013) via RivFishTIME (Comte et al., 2021). We used
158 data collected in 65 waterbodies consisting a total of 181 permanent sampling sites (2–10 sites
159 per waterbody) across Sweden in 1990 and 2018 (see Appendix S4 for site IDs and selection
160 criteria). The abundance of each fish species in each site was recorded as the number of
161 individuals per 100 m². We quantified the compositional variation among sites within each
162 waterbody based on the normalized abundance-based Whittaker's beta diversity using either
163 incidence (presence–absence) or abundance data. The incidence data was obtained by
164 transforming the abundance values larger than zero to one. We calculated the temporal changes in
165 beta diversity ($\Delta\beta$) and their additive components between 1990 and 2018. The components
166 representing species extinctions and colonizations (i.e., changes from presence to absence and
167 vice versa) are denoted as $\Delta\beta_E$ and $\Delta\beta_C$. Those that represent abundance losses and gains are
168 denoted as $\Delta\beta_L$ and $\Delta\beta_G$.

169 The incidence- and abundance-based approaches provided complementary insights into the
170 changes in beta diversity (Figure 3). While the incidence-based beta diversity showed no
171 temporal trend (Figure 3a), the abundance-based beta diversity significantly decreased from 1990
172 and 2018, as indicated by $\Delta\beta$ less than zero (Figure 3b). The loss and gain components ($\Delta\beta_L$ and
173 $\Delta\beta_G$) revealed that this homogenization of fish communities was explained by gains, but not

174 losses, in species abundances (Figure 3b). Partitioning $\Delta\beta$ into species-level components further
175 showed that the homogenization was largely caused by brown trout (*Salmo trutta*) (Figure 3d; see
176 Appendix S4 for the results of all species). The fact that the colonization component $\Delta\beta_C$ of
177 brown trout was not significant (Figure 3c) indicates that the homogenization did not result from
178 colonizations of brown trout to new sites. Rather, it was caused by the increased sizes of brown
179 trout populations (potentially associated with fishing restrictions and stocking; Almesjö & Limén,
180 2009) in sites where they were already present but in low abundances, leading to a more
181 spatially-uniform abundance distribution.

182

183 **4 | Discussion**

184 We developed a new method to partition the temporal changes in beta diversity into distinct
185 components that reflect the losses and gains in species abundances (Figure 1). **The method**
186 **provides a unified approach to analyze biotic homogenization and differentiation using both**
187 **incidence and abundance data. Application of our method to an empirical dataset revealed**
188 **different trends in incidence- and abundance-based beta diversity ($\Delta\beta_E$, $\Delta\beta_C$, $\Delta\beta_L$, and $\Delta\beta_G$)**
189 **(Figure 3). The two approaches collectively showed that gains in abundances, but not**
190 **colonization, of particular species made communities become more similar over time (Figure 3).**
191 **The results highlight that our partitioning method effectively identifies local population and**
192 **community processes embedded in regional biodiversity patterns.**

193 Moving forward, further generalizations of our temporal partitioning method are needed. In
194 this study, we partitioned Ružička and Bray–Curtis indices and the normalized abundance-based
195 Whittaker’s beta diversity. A promising next step will be to extend the method to beta diversity
196 based on Hill numbers (Hill, 1973; Jost, 2007; Chao & Chiu, 2016). Hill numbers link different
197 lines of beta diversity research together and unify multiple dissimilarity measures into a common
198 expression (Jost, 2007; Chao & Chiu, 2016; Chao et al., 2019). Temporal partitioning of Hill-
199 number-based beta diversity could thus give us a synthetic understanding of community
200 dynamics. Exploring the potential connections between our method and other partitioning
201 methods that are based on Hill numbers (Godsoe et al., 2021, 2022) would also be an important
202 way forward.

203 We expect our partitioning method to serve as a useful tool in both basic and applied
204 ecology. Specifically, the capability of our method to quantify species-level processes could help
205 conservation practitioners to assess the impacts of particular species on regional biodiversity
206 (e.g., increased abundance of an invasive nonnative species and consequent decreases in
207 endangered species). **Empirical ecologists could use the homogenization and differentiation**
208 **components of beta diversity to infer metacommunity processes and regional coexistence**
209 **mechanisms.** We believe that explicit analyses of the losses and gains in species abundances
210 bring deeper insights into ecological community structure across space and time.

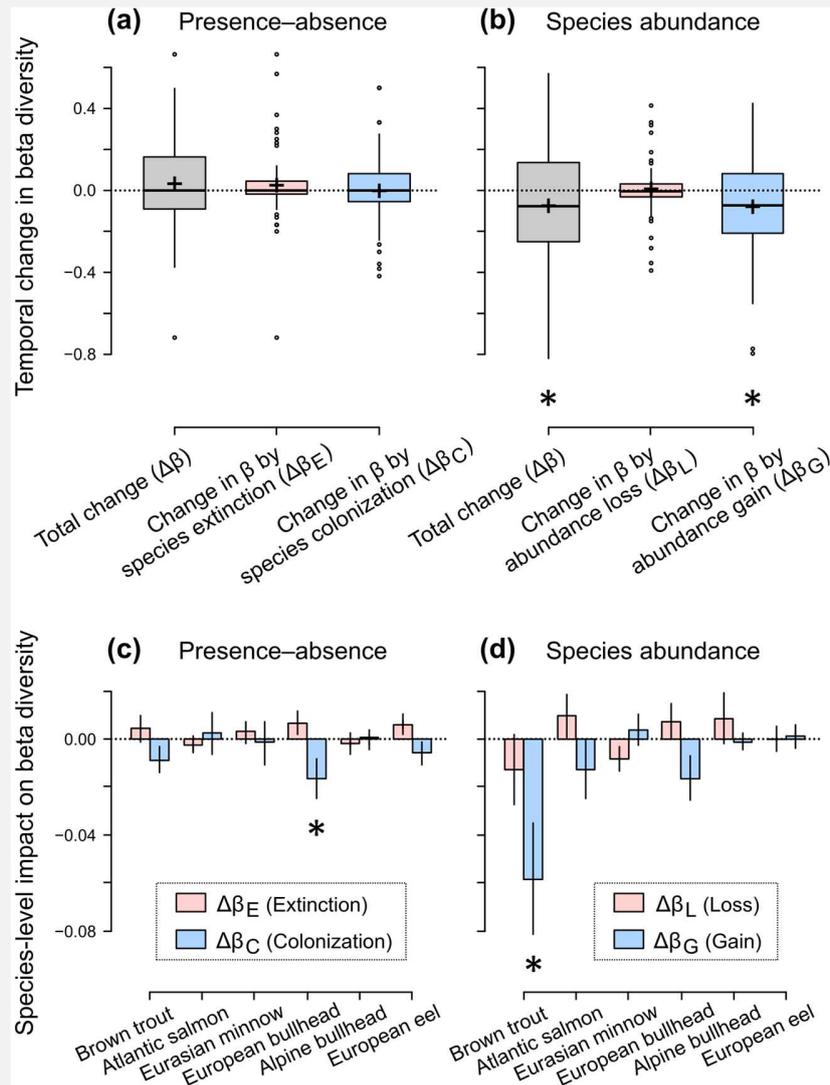


Figure 3. Temporal change in beta diversity and its components of riverine fish communities in 65 waterbodies across Sweden between 1990 and 2018. Beta diversity was defined as the compositional variation among multiple sampling sites within each waterbody. (a) Temporal changes in beta diversity based on species presence–absence and its extinction and colonization components. (b) Temporal changes in beta diversity based on species abundance and its loss and gain components. (c) Impacts of local extinctions and colonizations (i.e., changes from presence to absence and vice versa) of the six most abundant species (arranged in descending order) on beta diversity. (d) Impacts of abundance losses and gains of the six species on beta diversity. In the upper panels, the plus signs, horizontal lines, boxes, and circles indicate the means, medians, interquartile ranges (IQR), and outliers (values outside $1.5 \times \text{IQR}$), respectively. In the bottom panels, bars and lines show the means \pm standard errors. Asterisks indicate that the mean value was significantly different from zero (one-sample *t*-test; $P < 0.05$).

211 **AUTHORS' CONTRIBUTIONS**

212 ST conceived the study, derived the partitioning equations, and analyzed the data. ST wrote the
213 manuscript with inputs from RI and MWC. **All authors contributed to manuscript revision.**

214

215 **DATA ACCESSIBILITY**

216 The R package `ecopart` ('Ecological COmmunity PARTitioning' or 'Extinction and COlonization
217 PARTitioning') and an R script for extracting the Swedish fish community data from
218 RivFishTIME (Comte et al., 2021) are available at GitHub
219 (<https://github.com/communityecologist>). **The `ecopart` package can be installed using the `remotes`
220 package (Csardi et al., 2021): `remotes::install_github("communityecologist/ecopart")`.**

221

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SUPPORTING INFORMATION

Title: Partitioning the temporal changes in abundance-based beta diversity into loss and gain components

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Appendix S1: Derivation of partitioning equations: Pairwise dissimilarity

We first derive the equations to additively partition the temporal changes in Ružička and Bray–Curtis indices which are abundance-based, pairwise dissimilarity measures. We define the variables as follows:

$$\beta_{\text{Ruž}} = \frac{\sum_{i=1}^S \min(\alpha_{i1}, \alpha_{i2})}{\sum_{i=1}^S (\alpha_{i1} + \alpha_{i2})} \text{ Ružička index.}$$

$$\beta_{\text{BC}} = \frac{\sum_{i=1}^S \min(\alpha_{i1}, \alpha_{i2})}{\sum_{i=1}^S (2\alpha_{i1} + \alpha_{i2})} \text{ Bray–Curtis index.}$$

i	Species identity.
S	Number of species.
α_{ij}	Component of species abundance common to both sites.
$\alpha_{i\bar{j}}$	Component of species abundance unique to either site.
α_{ik}	Abundance of species i in site k .
$\alpha_{i1} - \alpha_{i2}$	Type 1: Amount of loss in α_{i1} in the site where α_{i2} was larger than that in the other site.
$\alpha_{i1} - \alpha_{i2}$	Type 2: An equal amount of loss in α_{i1} in both sites.
$\alpha_{i1} - \alpha_{i2}$ equal to,	Type 3: Amount of loss in α_{i1} in the site where α_{i2} was smaller than, or that in the other site.
$\alpha_{i2} - \alpha_{i1}$ to,	Type 4: Amount of gain in α_{i2} in the site where α_{i1} was larger than, or equal that in the other site.
$\alpha_{i2} - \alpha_{i1}$	Type 5: An equal amount of gain in α_{i2} in both sites.
$\alpha_{i2} - \alpha_{i1}$ the	Type 6: Amount of gain in α_{i2} in the site where α_{i1} was smaller than that in other site.
$\alpha_{i1} - \alpha_{i2}$ gain	Hidden dynamics: Amount of loss in α_{i1} in the site where it was larger and in α_{i2} in the other site where it was smaller.

See also Figures S1 and S2 for visual descriptions of the variables.

For brevity, we write the sum of a given variable across all species (1, 2, ..., S) using the uppercase letters (e.g., $\sum_{i=1}^S \alpha_{i1} = \alpha$ and $\sum_{i=1}^S \alpha_{i2} = \alpha'$). To distinguish the variables at $t = 1$ and $t = 2$, we add prime symbols to the latter cases (e.g. α'). From the definitions above, we can write

$$\Delta\alpha = \alpha' - \alpha = -\alpha_{11} - \alpha_{21} + \alpha_{12} + \alpha_{22}$$

$$\Delta \square = \square' - \square = -\square^{\square} + \square^{\square} + \square^{\square} - \square^{\square}.$$

The temporal changes in pairwise dissimilarity ($\Delta\beta^{(\lambda)} = \beta'_{Ru\check{z}} - \beta_{Ru\check{z}}$ when $\lambda = 1$, and $\beta^{(\lambda)} = \beta'_{BC} - \beta_{BC}$ when $\lambda = 2$) can then be written as

$$\begin{aligned} \Delta\beta^{(\lambda)} &= \Delta\beta^{(\lambda)'} - \Delta\beta^{(\lambda)} \\ &= \frac{\square'}{\lambda\square' + \square'} - \frac{\square}{\lambda\square + \square} \\ &= \frac{\lambda(\square\square' - \square'\square)}{(\lambda\square + \square)(\lambda\square' + \square')} \\ &= \frac{\lambda\square\square \left(\frac{\Delta\square}{\square} - \frac{\Delta\square}{\square} \right)}{(\lambda\square + \square)(\lambda\square' + \square')} \quad \because \square' = \square + \Delta\square, \square' = \square + \Delta\square \\ &= \frac{\lambda\square\square}{\underbrace{(\lambda\square + \square)(\lambda\square' + \square')}_{\square}} \times \left(\frac{-\square^{\square} + \square^{\square} + \square^{\square} - \square^{\square}}{\square} + \frac{\square^{\square} + \square^{\square} - \square^{\square} - \square^{\square}}{\square} \right), \end{aligned}$$

where \square and \square are both non-zero. Accordingly, the partitioning equation, without the hidden dynamics, reads

$$\begin{aligned} \Delta\beta^{(\lambda)} &= \Delta\beta^{(\lambda)'} - \Delta\beta^{(\lambda)} \\ &= \underbrace{-\frac{\square}{\square}}_{\Delta\beta_1} \square^{\square} + \underbrace{\frac{\square}{\square}}_{\Delta\beta_2} \square^{\square} + \underbrace{\left(\frac{\square}{\square} + \frac{\square}{\square} \right)}_{\Delta\beta_3} \square^{\square} + \underbrace{\frac{\square}{\square}}_{\Delta\beta_4} \square^{\square} + \underbrace{\frac{-\square}{\square}}_{\Delta\beta_5} \square^{\square} + \underbrace{\left(-\frac{\square}{\square} - \frac{\square}{\square} \right)}_{\Delta\beta_6} \square^{\square}. \end{aligned}$$

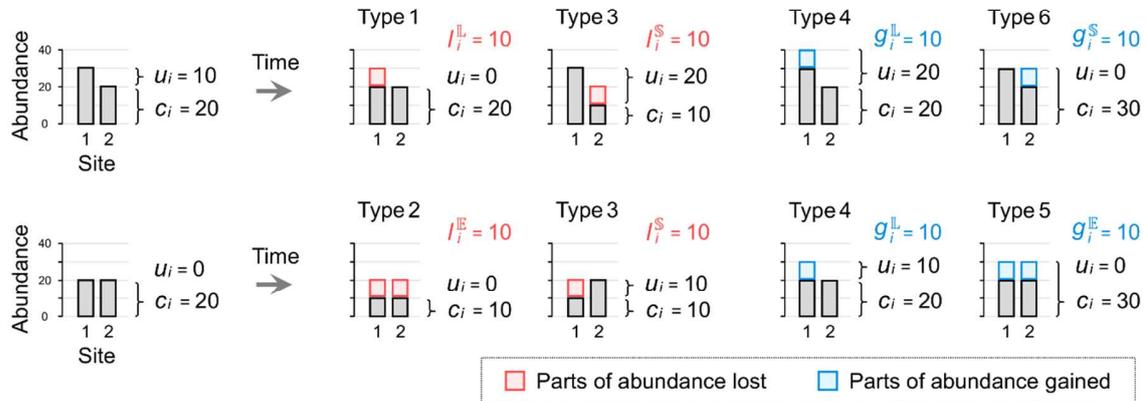
To account for hidden dynamics, we add D to the multipliers of the first and fourth terms in the above equation. Hidden dynamics refer to decreases in species abundance in the site where it was larger and offsetting increases in species abundance in the other site where it was smaller (Figure S2). By adding D to the equation, we get Equation 1 in the main text.

(a) Pairwise dissimilarity measures

Ružička $\beta_{Ruž} = \frac{\sum_{i=1}^S u_i}{\sum_{i=1}^S (c_i + u_i)}$ Bray–Curtis $\beta_{BC} = \frac{\sum_{i=1}^S u_i}{\sum_{i=1}^S (2c_i + u_i)}$

i : Species identity
 c_i : Parts of abundance common to both sites
 u_i : Parts of abundance unique to either sites

(b) Types of losses and gains in species abundance



(c) Consequences of abundance losses and gains on dissimilarity

Type	Description	Temporal changes in ...		
		c_i	u_i	$\beta_{Ruž}$ and β_{BC}
1	Abundance (a_i) decreases in the site where a_i is larger (L) than that in the other site.	0	$-I_i^L$	–
2	a_i decreases by equal amount (E) in both sites.	$-I_i^E$	0	+
3	a_i decreases in the site where a_i is smaller (S) than, or equal to, that in the other site.	$-I_i^S$	$+I_i^S$	+
4	a_i increases in the site where a_i is larger (L) than, or equal to, that in the other site.	0	$+g_i^L$	+
5	a_i increases by equal amount (E) in both sites.	$+g_i^E$	0	–
6	a_i increases in the site where a_i is smaller (S) than that in the other site.	$+g_i^S$	$-g_i^S$	–

Figure S1. Schematic representation of the temporal changes in spatial beta diversity and types of losses and gains in species abundances that drive the changes. (a) Ružička and Bray–Curtis dissimilarity indices. (b) Examples of abundances losses and gains categorized into six types based on their impacts on beta diversity. (c) Descriptions of the six types of abundances losses and gains.

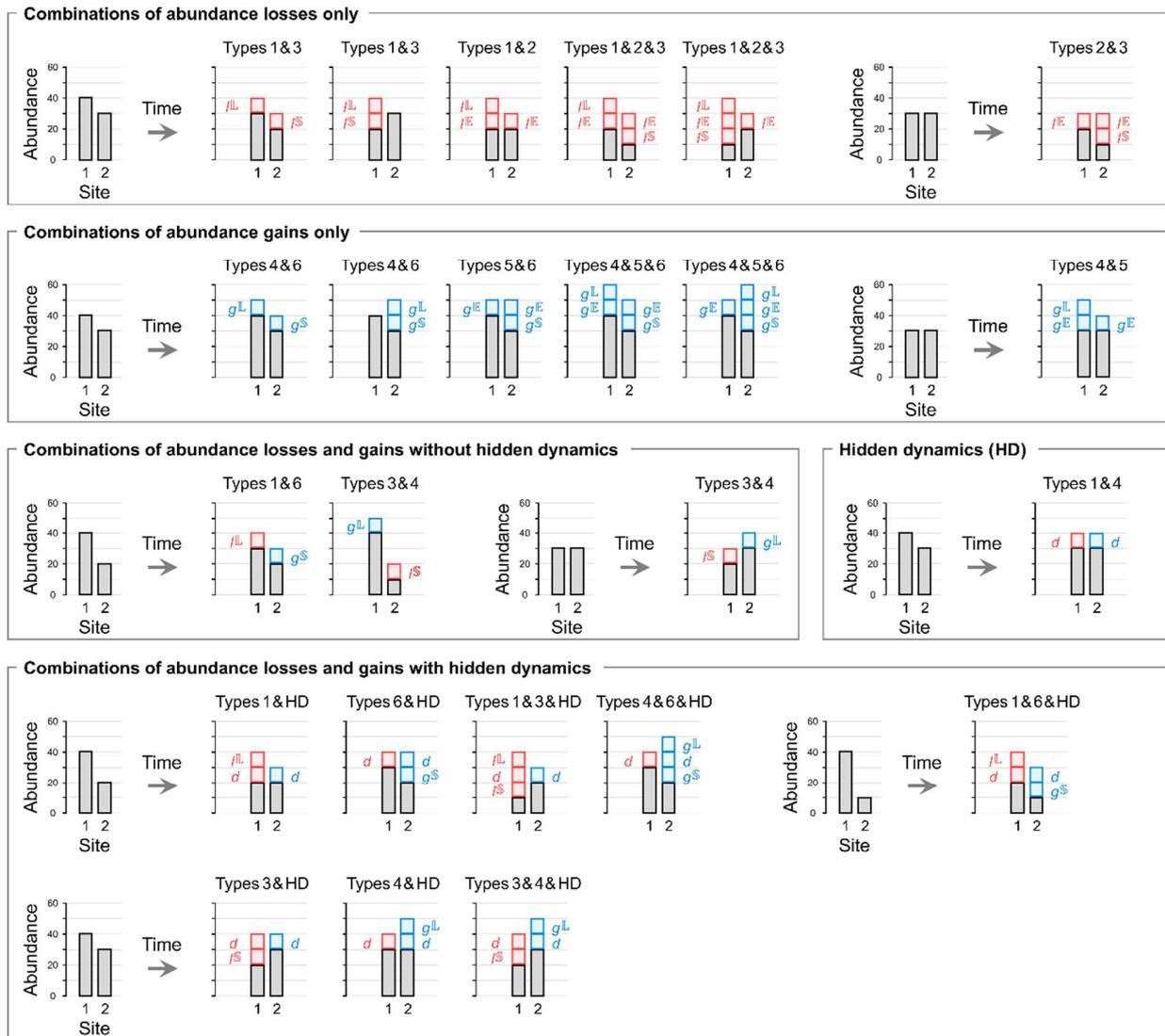


Figure S2. Possible combinations of abundance losses and gains including hidden dynamics in the case of two sites. In total, there are 32 possible ways of abundance losses and gains; i.e., the 8 types shown in Figure S1 and the 24 combinations shown here.

Appendix S2: Sensitivity analyses

We conducted sensitivity analyses to verify the impacts of losses and gains in species abundances on $\Delta\beta$ components ($\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$, $\Delta\beta_6$, $\Delta\beta_{L-}$, $\Delta\beta_{L+}$, $\Delta\beta_{G-}$, and $\Delta\beta_{G+}$). We varied nine variables L^L , L^E , L^S , G^L , G^E , G^S , D , C , and U one by one from 0 to 100 while fixing the others at 5. We then calculated the sizes of the components based on Ružička and Bray–Curtis indices ($\beta_{Ruž}$ and β_{BC}). Note that the components of β_{BC} and the normalized abundance-based Whittaker's beta (β_W) are mathematically identical (see Appendix S3). The sensitivity analyses we conducted here for abundance losses and gains are analogous to what we did for species extinctions and colonizations using presence–absence data (Tatsumi et al., 2021).

The sensitivity analyses confirmed that the component $\Delta\beta_{L-}$ ($\Delta\beta_1$) decreases with L^L (the loss in species abundance unique to either site), whereas the component $\Delta\beta_{L+}$ ($\Delta\beta_2$ and $\Delta\beta_3$) increases with L^E and L^S (the loss in species abundance common to both sites) (Figures S3a–c, S4a–c). Similarly, for colonization, $\Delta\beta_{G+}$ ($\Delta\beta_4$) increases with G^L (the gain in species abundance unique to either site), whereas $\Delta\beta_{G-}$ ($\Delta\beta_5$ and $\Delta\beta_6$) decreases with G^E and G^S (the gain in species abundance common to both sites) (Figures S3d–f, S4d–f). These results were similar to what we found with the portioning of extinction and colonization components (Tatsumi et al., 2021).

We also found that $\Delta\beta_3$ and $\Delta\beta_6$ change more largely than $\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_4$, and $\Delta\beta_5$ do in response to the varying values of L^L , L^E , L^S , G^L , G^E , G^S (Figures S3a–f, S4a–f). This finding agrees well with the fact that $\Delta\beta_3$ and $\Delta\beta_6$ reflect numerical changes in both unique and shared parts of species abundances (see types 3 and 6 in Figure S1), whereas the other $\Delta\beta$ components are only responsible for either unique or shared species (types 1, 2, 4, and 5). Furthermore, consistent with its definition, the hidden species dynamics (D) simultaneously decreased $\Delta\beta_1$ and increased $\Delta\beta_3$ without affecting the total $\Delta\beta$ (Figures S3g, S4g). The amount of species abundance common to both sites (constant C) caused no impact on $\Delta\beta$ but reduced the relative importance of other species (Figures S3h, S4h). Similarly, the amount of species abundance unique to either site (constant U) caused no impact on $\Delta\beta$ (Figures S3i, S4i). Again, these results were similar to what we found with the portioning of extinction and colonization components (Tatsumi et al., 2021).

Reference

Tatsumi, S., Iritani, R., Cadotte, M.W. (2021). Temporal changes in spatial variation: partitioning the extinction and colonisation components of beta diversity. *Ecology Letters* 24, 1063–1072.

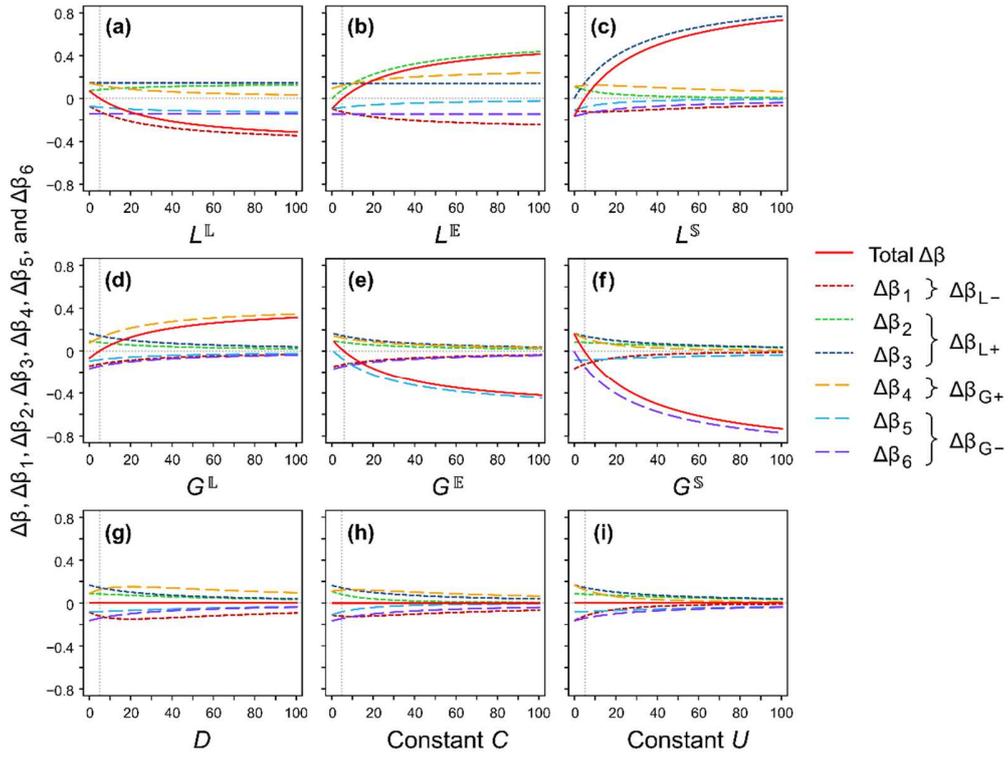


Figure S3. Sensitivity analyses of the response of temporal changes in Ružička index and its components to varying amount of species abundance common to either site and unique to both sites.

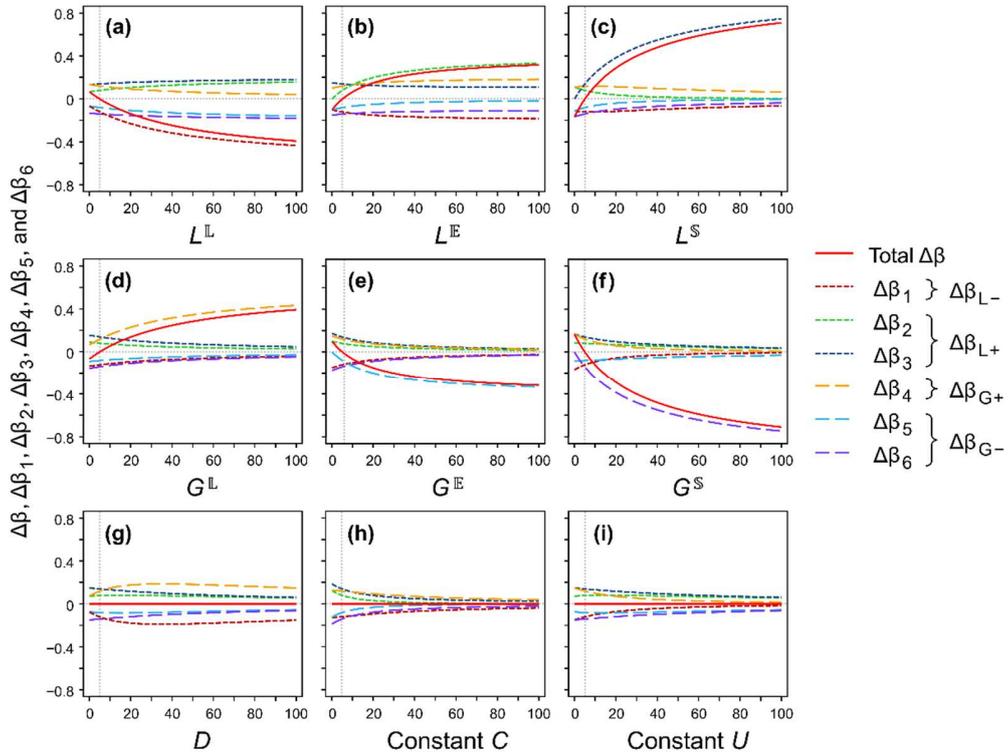


Figure S4. Sensitivity analyses of the response of temporal changes in Bray–Curtis index (which is mathematically identical to the normalized abundance-based Whittaker’s beta when $N = 2$) and its components to varying amount of species abundance common to either site and unique to both sites.

Appendix S3: Derivation of partitioning equations: Multisite variation

Our partitioning approach is applicable to multisite measures as well. For cases with more than two sites, averaging pairwise dissimilarities ($\beta_{Ru\check{z}}$ and β_{BC}) across all pairs of sites is a suboptimal approach due to the lack of their statistical independence (Baselga, 2010, 2017).

Here, we consider the normalized abundance-based Whittaker's beta (β_w) proposed by Baselga (2017). Harrison et al. (1992) defined the normalized incidence-based Whittaker's beta as $(\gamma/\bar{\alpha} - 1)/(\square - 1)$, where γ is the regional species richness, $\bar{\alpha}$ is the mean local species richness, and N is the number of sites. While the original Whittaker's beta ($\gamma/\bar{\alpha}$) ranges in the interval $[1, N]$ (Whittaker, 1960), the normalized measure ranges in the interval $[0, 1]$ (Harrison et al., 1992). This normalized measure has been extended by Baselga (2017) to account for abundance. β_w and other variables are defined as follows:

$\beta_w = \frac{\square \cdot \sum_{\square} \max\{\square_{\square\square}\} - \square}{(\square - 1)\square}$	Baselga's beta, or the normalized abundance-based Whittaker's beta.
\square	Number of sites.
\square	Number of species.
$\square_{\square\square}$	Abundance of species i in site k .
$\max\{\square_{\square\square}\}$ denoted as \square_{\square} .	The maximum abundance of species i across all the sites. Also denoted as \square_{\square} .
\square	Total abundance of all species in all sites (i.e., $\square = \sum_{\square=1}^{\square} \sum_{\square=1}^{\square} \square_{\square\square}$).
$\square_{\square+}$	Abundance of species i summed across all sites (i.e., $\square_{\square+} = \sum_{\square=1}^{\square} \square_{\square\square}$).
$\square_{\square\square}$	Amount of loss in the maximum abundance of species i (\square_{\square}) in n sites.
$\square_{\square\square}$ abundance n sites.	Amount of loss in $\square_{\square+}$ without causing any change in \square_{\square} — i.e., loss that does not affect the maximum abundance of species i in n sites.
$\square_{\square\square}$	Amount of gain in the maximum abundance of species i (\square_{\square}) in n sites.
$\square_{\square\square}$ abundance n sites.	Amount of gain in $\square_{\square+}$ without causing any change in \square_{\square} — i.e., gain that does not affect the maximum abundance of species i in n sites.
$\square_{\square\square\square}$ and the	Amount of losses in the abundance of species i in v -number of sites and the
	offsetting gains in w -number of sites occurring within the same time interval.

We extend the variables \square_{\square} , \square_{\square} , \square_{\square} , \square_{\square} , \square_{\square} , and \square_{\square} , defined earlier (Appendix S1; Figures S1, S2) to denote the temporal changes in the maximum abundance (m_i) and the total abundance (a_{i+}) of species i . First, we extend \square_{\square} to denote the decrease in species abundance associated with both m_i and a_{i+} . This type of abundance loss decreases m_i by \square_{\square} . For example, m_i decreases by 10 when $\square_{\square} = 10$. The amount of decrease in a_{i+} , on the other hand, depends on the number of sites in which a given species i showed its maximum abundance at $t = 1$. This dependency can be taken explicitly into account by adding a subscript n to \square_{\square} , such that $\square_{\square\square}$ denotes the decrease in the maximum abundance across n sites. This type of abundance loss decreases a_{i+} by $\square \cdot \square_{\square\square}$. For instance, a_{i+} decreases by 10 when $\square_{\square 1} = 10$ and decreases by 20 when $\square_{\square 2} =$

10, whereas m_i decreases by 10 in either case. Similarly, we define $\Delta_{i, n}^{\square}$ to denote the increase in the maximum abundance of species i across n sites.

We extend the definition of $\Delta_{i, n}^{\square}$ to denote the abundance loss in all sites (N) across which a given species i showed its maximum abundance at $t = 1$. In this case, m_i and a_{i+} decrease by $\Delta_{i, n}^{\square}$ and $\Delta_{i, n}^{\square} \cdot \Delta_{i, n}^{\square}$, respectively. Thus, $\Delta_{i, n}^{\square}$ can be seen as a special case of $\Delta_{i, n}^{\square}$ when $n = N$. We therefore rewrite $\Delta_{i, n}^{\square}$ as $\Delta_{i, n}^{\square}$ hereafter. Similarly, we rewrite $\Delta_{i, n}^{\square}$ as $\Delta_{i, n}^{\square}$ for the gain in abundance across all sites in which a given species i showed its maximum abundance at $t = 2$.

We define $\Delta_{i, n}^{\square}$ as the abundance loss associated with the decrease in a_{i+} but not m_i . We use the subscript n to let $\Delta_{i, n}^{\square}$ denote the abundance loss in n sites across which a given species i showed smaller abundance than, or equal abundance to, m_i at both $t = 1$ and 2. This type of abundance loss decreases a_{i+} by $\Delta_{i, n}^{\square} \cdot \Delta_{i, n}^{\square}$ but does not alter m_i . Similarly, we define $\Delta_{i, n}^{\square}$ as the increase in abundance across n sites where species i showed smaller abundance than, or equal abundance to, m_i at both $t = 1$ and 2.

Hidden dynamics can occur not only in the case of two sites ($N = 2$) but also multiple sites ($\square \geq 3$). To account for this, we extend the definition of hidden dynamics as the abundance losses in the site(s) where a given species i showed its maximum abundance at $t = 1$ and the offsetting gains in the other site(s). By adding subscripts v and w to d_i , we write $d_{i, v, w}$ for the abundance losses in v -number of sites and the offsetting gains in w -number of sites occurring within the same time interval ($\square \geq 1$, $\square \geq 1$, and $\square + \square \leq \square$).

Again, for brevity, we write the sum of a given variable across all species (1, 2, ..., S) using the uppercase letters (e.g., $\sum_{i=1}^{\square} \max\{\Delta_{i, n}^{\square}\} = \sum_{i=1}^{\square} \Delta_{i, n}^{\square} = \Delta$, $\sum_{i=1}^{\square} \Delta_{i, n}^{\square} = \Delta_{i, n}^{\square}$, and $\sum_{i=1}^{\square} \Delta_{i, n}^{\square} = \Delta_{i, n}^{\square}$). Equation 1 in the main text can be rewritten using the extended definitions by replacing L^L , L^E , L^S , G^L , G^E , G^S , and D with Δ_1^L , Δ_2^L , Δ_1^E , Δ_1^E , Δ_2^E , Δ_1^S , and D_{11} , respectively.

Two-site cases

To partition β_w , we first consider the case of two communities ($N = 2$). The temporal changes in M and A can be written as

$$\begin{aligned}\Delta \square &= \square' - \square = -\Delta_1^L - \Delta_2^L + \Delta_1^E + \Delta_2^E \\ \Delta \square &= \square' - \square = -\Delta_1^L - 2\Delta_2^L - \Delta_1^E + \Delta_1^E + 2\Delta_2^E + \Delta_1^S.\end{aligned}$$

The temporal changes in β_w when $\square = 2$ can then be partitioned as

$$\begin{aligned}\Delta \beta_w &= \beta_w' - \beta_w \\ &= \frac{\Delta \square' - \square'}{(\square - 1)\square'} - \frac{\Delta \square - \square}{(\square - 1)\square} \\ &= \frac{\Delta \square' \square - \Delta \square \square'}{(\square - 1)\square \square'} \\ &= \frac{\Delta \square \left(\frac{\Delta \square}{\square} - \frac{\Delta \square}{\square} \right)}{(\square - 1)\square'} \quad \because \square' = \square + \Delta \square, \square' = \square + \Delta \square \\ &= \frac{\Delta \square}{(\square - 1)\square'} \times \left(\frac{-\Delta_1^L - \Delta_2^L + \Delta_1^E + \Delta_2^E}{\square} + \frac{\Delta_1^E + 2\Delta_2^E + \Delta_1^S - \Delta_1^L - 2\Delta_2^L - \Delta_1^E}{\square} \right),\end{aligned}$$

where M and A are both non-zero. Accordingly, we get the partitioning equation, without the hidden dynamics, which reads

$$\begin{aligned}\Delta\beta_W &= \beta'_W - \beta_W \\ &= \underbrace{\left(\frac{-\square}{\square} + \frac{\square}{\square}\right) \square_I}_{\Delta\beta_1} + \underbrace{\left(\frac{-\square}{\square} + \frac{2\square}{\square}\right) \square_2}_{\Delta\beta_2} + \underbrace{\frac{\square}{\square} \square_I}_{\Delta\beta_3} + \underbrace{\left(\frac{\square}{\square} - \frac{\square}{\square}\right) \square_I}_{\Delta\beta_4} + \underbrace{\left(\frac{\square}{\square} - \frac{2\square}{\square}\right) \square_2}_{\Delta\beta_5} + \underbrace{\frac{-\square}{\square} \square_I}_{\Delta\beta_6}.\end{aligned}$$

As we did for pairwise dissimilarity ($\beta_{Ru\check{z}}$ and β_{BC}), the hidden dynamics can be accounted for by adding D to the multipliers of the first and fourth terms:

$$\begin{aligned}\Delta\beta_W &= \beta'_W - \beta_W \\ &= \underbrace{\left(\frac{-\square}{\square} + \frac{\square}{\square}\right) (\square_I + \square_{11})}_{\Delta\beta_1} + \underbrace{\left(\frac{-\square}{\square} + \frac{2\square}{\square}\right) \square_2}_{\Delta\beta_2} + \underbrace{\frac{\square}{\square} \square_I}_{\Delta\beta_3} + \underbrace{\left(\frac{\square}{\square} - \frac{\square}{\square}\right) (\square_I + \square_{11})}_{\Delta\beta_4} \\ &\quad + \underbrace{\left(\frac{\square}{\square} - \frac{2\square}{\square}\right) \square_2}_{\Delta\beta_5} + \underbrace{\frac{-\square}{\square} \square_I}_{\Delta\beta_6}.\end{aligned}$$

We define the six terms as the loss and gain components of temporal changes in the normalized abundance-based Whittaker's beta ($\Delta\beta_W$) at $N = 2$.

Note that β_W and β_{BC} are identical when $\square = 2$ (Beselga, 2017):

$$\begin{aligned}\beta_W &= \frac{\square\square - \square}{(\square - I)\square} \\ &= \frac{2(\square + \square) - (2\square + \square)}{2\square + \square} \quad \because \square = \square + \square, \square = 2\square + \square \\ &= \frac{\square}{2\square + \square} = \beta_{BC}.\end{aligned}$$

The six components of $\Delta\beta_W$ and $\Delta\beta_{BC}$ of ($\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$, and $\Delta\beta_6$) are also identical to each other when $\square = 2$:

$$\begin{aligned}\Delta\beta_1 &= \left(\frac{-\square}{\square} + \frac{\square}{\square}\right) \square_I \\ &= \left(\frac{-2}{\square'} + \frac{2\square}{\square\square'}\right) \square_I = \frac{2\square - 2\square}{\square\square'} \square_I = \frac{-2\square}{(2\square + \square)(2\square' + \square')} \square_I \\ &= -\frac{\square}{\square} \square_I\end{aligned}$$

$$\begin{aligned}\Delta\beta_2 &= \left(\frac{-\square}{\square} + \frac{2\square}{\square}\right) \square_2 \\ &= \left(\frac{-2}{\square'} + \frac{4\square}{\square\square'}\right) \square_2 = \frac{2\square}{(2\square + \square)(2\square' + \square')} \square_2 \\ &= \frac{\square}{\square} \square_2\end{aligned}$$

$$\Delta\beta_3 = \frac{\square}{\square} \square_I$$

$$\begin{aligned}
&= \frac{2\alpha}{\alpha\alpha} \alpha_I^\alpha = \frac{2\alpha + 2\alpha}{(2\alpha + \alpha)(2\alpha' + \alpha)} \alpha_I^\alpha \\
&= \left(\frac{\alpha}{\alpha} + \frac{\alpha}{\alpha}\right) \alpha_I^\alpha.
\end{aligned}$$

We also obtain $\Delta\beta_4 = \left(\frac{\alpha}{\alpha} - \frac{\alpha}{\alpha}\right) \alpha_I^\alpha = \frac{\alpha}{\alpha} \alpha_I^\alpha$, $\Delta\beta_5 = \left(\frac{\alpha}{\alpha} - \frac{\alpha}{\alpha}\right) \alpha_I^\alpha = \frac{\alpha}{\alpha} \alpha_I^\alpha$, and $\Delta\beta_6 = \left(\frac{\alpha}{\alpha} - \frac{\alpha}{\alpha}\right) \alpha_I^\alpha = \frac{\alpha}{\alpha} \alpha_I^\alpha$ by replacing α_I^α with $-\alpha_I^\alpha$, α_2^α with $-\alpha_2^\alpha$, and α_I^α with $-\alpha_I^\alpha$ in the above equations, respectively.

Three-site cases

Let us next expand the β_W -based partitioning equations to the case of three sites. For the sake of simplicity, we first leave out the hidden dynamics. When $\alpha = 3$, there will be one, two or three site(s) in which species i shows its maximum abundance (α_α). The subscript n of $\alpha_{\alpha\alpha}^\alpha$ and $\alpha_{\alpha\alpha}^\alpha$ will thus range from 1 to 3: $\alpha_{\alpha 1}^\alpha$, $\alpha_{\alpha 2}^\alpha$, $\alpha_{\alpha 3}^\alpha$, $\alpha_{\alpha 1}^\alpha$, $\alpha_{\alpha 2}^\alpha$, and $\alpha_{\alpha 3}^\alpha$. On the other hand, there will be one or two site(s) in which species i shows abundance less than α_α . The temporal changes in species abundance that do not affect α_α can thus occur in 1 or 2 sites: $\alpha_{\alpha 1}^\alpha$, $\alpha_{\alpha 2}^\alpha$, $\alpha_{\alpha 1}^\alpha$, and $\alpha_{\alpha 2}^\alpha$. As such, we get

$$\begin{aligned}
\alpha\alpha &= \alpha' - \alpha = -\alpha_I^\alpha - \alpha_2^\alpha - \alpha_3^\alpha + \alpha_I^\alpha + \alpha_2^\alpha + \alpha_3^\alpha \\
\alpha\alpha &= \alpha' - \alpha = -\alpha_I^\alpha - 2\alpha_2^\alpha - 3\alpha_3^\alpha - \alpha_I^\alpha - 2\alpha_2^\alpha + \alpha_I^\alpha + 2\alpha_2^\alpha + 3\alpha_3^\alpha + \alpha_I^\alpha + 2\alpha_2^\alpha.
\end{aligned}$$

The temporal changes in β_W when $\alpha = 3$ can thus be partitioned as

$$\begin{aligned}
\Delta\beta_W &= \beta'_W - \beta_W \\
&= \frac{\alpha\alpha}{(\alpha - I)\alpha} \times \left(\frac{\Delta\alpha}{\alpha} - \frac{\Delta\alpha}{\alpha}\right) \\
&= \underbrace{\left(\frac{-\alpha}{\alpha} + \frac{\alpha}{\alpha}\right) \alpha_I^\alpha}_{\Delta\beta_{L-}} + \underbrace{\left(\frac{-\alpha}{\alpha} + \frac{2\alpha}{\alpha}\right) \alpha_2^\alpha}_{\Delta\beta_{L-} \text{ or } \Delta\beta_{L+}} + \underbrace{\left(\frac{-\alpha}{\alpha} + \frac{3\alpha}{\alpha}\right) \alpha_3^\alpha + \frac{\alpha}{\alpha} \alpha_I^\alpha + \frac{2\alpha}{\alpha} \alpha_2^\alpha}_{\Delta\beta_{L+}} \\
&\quad + \underbrace{\left(\frac{\alpha}{\alpha} - \frac{\alpha}{\alpha}\right) \alpha_I^\alpha}_{\Delta\beta_{G+}} + \underbrace{\left(\frac{\alpha}{\alpha} - \frac{2\alpha}{\alpha}\right) \alpha_2^\alpha}_{\Delta\beta_{G-} \text{ or } \Delta\beta_{G+}} + \underbrace{\left(\frac{\alpha}{\alpha} - \frac{3\alpha}{\alpha}\right) \alpha_3^\alpha + \frac{-\alpha}{\alpha} \alpha_I^\alpha + \frac{-2\alpha}{\alpha} \alpha_2^\alpha}_{\Delta\beta_{G-}}
\end{aligned}$$

Here, the terms are no longer categorized *a priori* into $\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$, and $\Delta\beta_6$. This is because when $N \geq 3$, some of the terms take either negative or positive values depending on the sizes of A and M . The terms can, however, be summed by groups in such a way that they represent homogenization and differentiation driven by abundance losses and gains ($\Delta\beta_{L-}$, $\Delta\beta_{L+}$, $\Delta\beta_{G-}$, and $\Delta\beta_{G+}$).

To explain why some terms can be either negative or positive, let us take the terms $\left(\frac{-q}{M} + \frac{q}{A}\right) L_1^{\mathbb{L}}$, $\left(\frac{-q}{M} + \frac{2q}{A}\right) L_2^{\mathbb{L}}$, and $\left(\frac{-q}{M} + \frac{3q}{A}\right) L_3^{\mathbb{L}}$ as examples. The variables $L_1^{\mathbb{L}}$, $L_2^{\mathbb{L}}$, and $L_3^{\mathbb{L}}$ indicate the sum of decreases in m_i in one, two, and three sites, respectively. The relative size of A to M is minimized when each species is present only in one site ($A = M$) and is maximized when each species shows the same abundance across all three sites (i.e., maximum abundances found in all sites; $A = 3M$). Thus, $\left(\frac{-q}{M} + \frac{q}{A}\right) L_1^{\mathbb{L}}$ is always nonpositive and $\left(\frac{-q}{M} + \frac{3q}{A}\right) L_3^{\mathbb{L}}$ is always nonnegative. These

mathematical results agree well with our intuition that the loss of species abundance unique to a single site results in biotic homogenization, whereas the loss of species abundance common to all sites leads to differentiation (Socolar et al., 2016; Tatsumi et al., 2020, 2021). On the other hand, $\left(\frac{-q}{M} + \frac{2q}{A}\right)L_2^{\parallel}$ can change its sign depending on the balance between A and M . This reflects the fact that the loss of species abundance unique to an intermediate number of sites can either drive homogenization or differentiation depending on the abundance distribution of all species across all sites.

We now consider the hidden dynamics when $\square = 3$. As described above, when $\square = 2$, there is only one possible combination of abundance loss and gain that could occur within the same time interval — i.e., an abundance loss in the site where species i showed its maximum abundance (\square_{\square}) and an offsetting abundance gain in the other site. When $\square = 3$, the number of possible combinations increases to three — i.e., an abundance loss(es) in one or two site(s) where species i showed \square_{\square} and an offsetting abundance gain(s) in the other one or two site(s). We denote the number of sites that corresponds such abundance losses and gains as v and w , respectively, where $\square \geq 1$, $\square \geq 1$, and $v + \square \leq \square$.

We write $\square_{\square\square}$ for the abundance losses in v -number of sites and the offsetting gains in w -number of sites occurring within the same time interval. The amount of change in $\Delta\beta$ driven by $\square_{\square\square}$ is equivalent to that cause by $\square_{\square}^{\square}$ and $\square_{\square}^{\square}$. By adding the three possible $\square_{\square\square}$ (i.e., \square_{11} , \square_{12} , and \square_{21}) to the corresponding terms in the equation above, the temporal changes in β_{\square} when $\square = 3$ can be partitioned as

$$\begin{aligned} \Delta\beta_{\square} &= \beta'_{\square} - \beta_{\square} \\ &= \underbrace{\left(\frac{-\square}{\square} + \frac{\square}{\square}\right)(\square_1^{\square} + \square_{11} + \square_{12})}_{\Delta\beta_{L-}} + \underbrace{\left(\frac{-\square}{\square} + \frac{2\square}{\square}\right)(\square_2^{\square} + \square_{21})}_{\Delta\beta_{L-} \text{ or } \Delta\beta_{L+}} \\ &\quad + \underbrace{\left(\frac{-\square}{\square} + \frac{3\square}{\square}\right)\square_3^{\square} + \frac{\square}{\square}\square_1^{\square} + \frac{2\square}{\square}\square_2^{\square}}_{\Delta\beta_{L+}} \\ &+ \underbrace{\left(\frac{\square}{\square} - \frac{\square}{\square}\right)(\square_1^{\square} + \square_{11} + \square_{21})}_{\Delta\beta_{G+}} + \underbrace{\left(\frac{\square}{\square} - \frac{2\square}{\square}\right)(\square_2^{\square} + h\square_{12})}_{\Delta\beta_{G-} \text{ or } \Delta\beta_{G+}} \\ &\quad + \underbrace{\left(\frac{\square}{\square} - \frac{3\square}{\square}\right)\square_3^{\square} + \frac{-\square}{\square}\square_1^{\square} + \frac{-2\square}{\square}\square_2^{\square}}_{\Delta\beta_{G-}}. \end{aligned}$$

Generalization: N -site cases

We now generalize the β_{\square} -based partitioning equations to the case of N sites. Again, for the sake of simplicity, we first leave out the hidden dynamics. When N , there will be $1, 2, \dots, N$ sites in which species i shows its maximum abundance (\square_{\square}). Thus, as we saw in the case of $\square = 3$, the subscript \square of $\square_{\square\square}$ and $\square_{\square}^{\square}$ will range from 1 to N : $\square_{\square 1}^{\square}, \square_{\square 2}^{\square}, \dots, \square_{\square \square}^{\square}$ and $\square_{\square 1}^{\square}, \square_{\square 2}^{\square}, \dots, \square_{\square \square}^{\square}$. On the other hand, there will be $1, 2, \dots, \square - 1$ sites in which species i shows abundance less than \square_{\square} . The temporal changes in species abundance that do not affect \square_{\square} can thus occur in $1, 2, \dots, \square - 1$ sites: $\square_{\square 1}^{\square}, \square_{\square 2}^{\square}, \dots, \square_{\square(\square-1)}^{\square}$ and $\square_{\square 1}^{\square}, \square_{\square 2}^{\square}, \dots, \square_{\square(\square-1)}^{\square}$. We thus get

$$\Delta\square = \square' - \square = - \sum_{\square=1}^{\square} \square_{\square}^{\square} + \sum_{\square=1}^{\square} \square_{\square}^{\square}$$

$$\beta_{\square} = \beta'_{\square} - \beta_{\square} = - \sum_{\square=1}^{\square} \beta_{\square} \beta_{\square} - \sum_{\square=1}^{\square-1} \beta_{\square} \beta_{\square} + \sum_{\square=1}^{\square} \beta_{\square} \beta_{\square} + \sum_{\square=1}^{\square-1} \beta_{\square} \beta_{\square}.$$

The temporal changes in β_{\square} can thus be partitioned as

$$\begin{aligned} \Delta\beta_{\square} &= \beta'_{\square} - \beta_{\square} \\ &= \frac{\beta_{\square}}{(\square - 1)\beta_{\square}} \times \left(\frac{\Delta\beta_{\square}}{\beta_{\square}} - \frac{\Delta\beta_{\square}}{\beta_{\square}} \right) \\ &= \underbrace{\sum_{\square=1}^{\square} \left(\frac{-\beta_{\square}}{\beta_{\square}} + \frac{\beta_{\square}}{\beta_{\square}} \right) \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square-} \text{ or } \Delta\beta_{\square+}} + \underbrace{\sum_{\square=1}^{\square-1} \frac{\beta_{\square}}{\beta_{\square}} \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square+}} + \underbrace{\sum_{\square=1}^{\square} \left(\frac{\beta_{\square}}{\beta_{\square}} - \frac{\beta_{\square}}{\beta_{\square}} \right) \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square-} \text{ or } \Delta\beta_{\square+}} + \underbrace{\sum_{\square=1}^{\square-1} \frac{-\beta_{\square}}{\beta_{\square}} \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square-}}. \end{aligned}$$

Finally, let us consider the generalization of the hidden dynamics. The hidden dynamics can occur in such a way that the abundance of species i decreases in 1, 2, ..., or $\square - 1$ sites where it showed is maximum abundance (β_{\square}) and increases in the other 1, 2, ..., or $\square - 1$ sites. As defined above, we write β_{\square} for the abundance losses in v -number of sites and the offsetting gains in w -number of sites occurring within the same time interval. The possible combinations of v and w that meet the conditions $v \geq 1$, $w \geq 1$, and $v + w \leq \square$ equals $\sum_{\square=1}^{\square} \beta_{\square} + \sum_{\square=1}^{\square-1} \beta_{\square} + \sum_{\square=1}^{\square-2} \beta_{\square} + \dots + \sum_{\square=1}^{\square-1} \beta_{\square}$. By adding all the possible β_{\square} (i.e., β_{11} , β_{12} , β_{13} , ..., $\beta_{1(\square-1)}$, β_{21} , β_{22} , ..., $\beta_{2(\square-2)}$, β_{31} , ..., $\beta_{(\square-2)1}$, $\beta_{(\square-2)2}$, $\beta_{(\square-1)1}$) to the corresponding multipliers (β_{\square} and β_{\square}) in the equation above, the temporal changes in β_{\square} at any number of sites (N) can be partitioned as

$$\begin{aligned} \Delta\beta_{\square} &= \beta'_{\square} - \beta_{\square} \\ &= \underbrace{\sum_{\square=1}^{\square} \left(\frac{-\beta_{\square}}{\beta_{\square}} + \frac{\beta_{\square}}{\beta_{\square}} \right) \beta_{\square} \beta_{\square} + \sum_{\{\square, \square | \square + \square \leq \square\}} \left(\frac{-\beta_{\square}}{\beta_{\square}} + \frac{\beta_{\square}}{\beta_{\square}} \right) \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square-} \text{ or } \Delta\beta_{\square+}} + \underbrace{\sum_{\square=1}^{\square-1} \frac{\beta_{\square}}{\beta_{\square}} \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square+}} \\ &+ \underbrace{\sum_{\square=1}^{\square} \left(\frac{\beta_{\square}}{\beta_{\square}} - \frac{\beta_{\square}}{\beta_{\square}} \right) \beta_{\square} \beta_{\square} + \sum_{\{\square, \square | \square + \square \leq \square\}} \left(\frac{\beta_{\square}}{\beta_{\square}} - \frac{\beta_{\square}}{\beta_{\square}} \right) \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square-} \text{ or } \Delta\beta_{\square+}} + \underbrace{\sum_{\square=1}^{\square-1} \frac{-\beta_{\square}}{\beta_{\square}} \beta_{\square} \beta_{\square}}_{\Delta\beta_{\square-}} \end{aligned}$$

The terms $\Delta\beta_{\square-}$ and $\Delta\beta_{\square+}$ indicate homogenization and differentiation, respectively, caused by abundance losses. Similarly, $\Delta\beta_{\square-}$ and $\Delta\beta_{\square+}$ represent homogenization and differentiation, respectively, caused by abundance gains.

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Appendix S4: Swedish fish community dataset

We retrieved the riverine fish community data from the Swedish Electrofishing Register database (Sers, 2013) via RivFishTIME (Comte et al., 2021) which is publicly available at the iDiv Biodiversity Portal (<https://doi.org/10.25829/ividiv.1873-10-4000>). The Swedish Electrofishing Register database consists of fish community data from 33,538 electrofishing surveys in 2,992 sites across Sweden from 1951 to 2018 (as of December 19, 2021). The number of sites surveyed per year increased from 1951 to ~2005 and has remained roughly constant since then (Figure S5).

In our analyses, we used the data collected in 1990 and 2018 considering the optimal balance between the number of sites surveyed per year (i.e., the number of samples) and the length of time separating the survey years. We selected permanent sites that were surveyed in both 1990 and 2018. We excluded waterbodies in which only one site was surveyed, since we defined beta diversity as the compositional variation among multiple sites ($n \geq 2$) within each waterbody. These criteria left us with 181 permanent sites across 65 waterbodies in 1990 and 2018. There were 23 fish species found in these sites. Note that, due the intense data filtering, the results of fish community dynamics shown in this study may not represent the general trends found using the whole dataset. The impacts of local extinctions and colonizations (i.e., changes from presence to absence and vice versa) and abundance losses and gains on beta diversity of individual species are shown in Figure S6. An R script for extracting and formatting the fish community data is available at GitHub (<https://github.com/communityecologist>).

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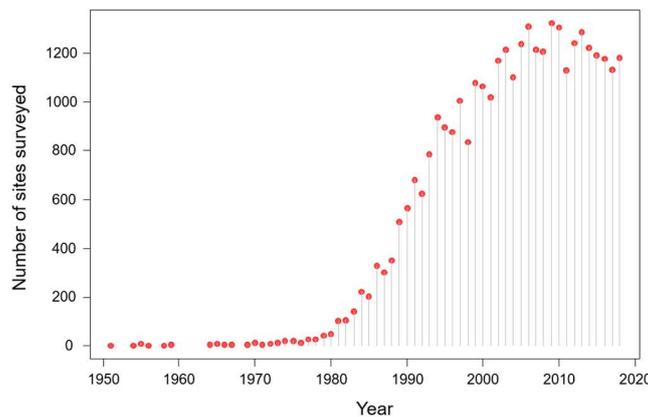


Figure S5. Number of sites surveyed per year in the Swedish Electrofishing Register database (Sers, 2013).

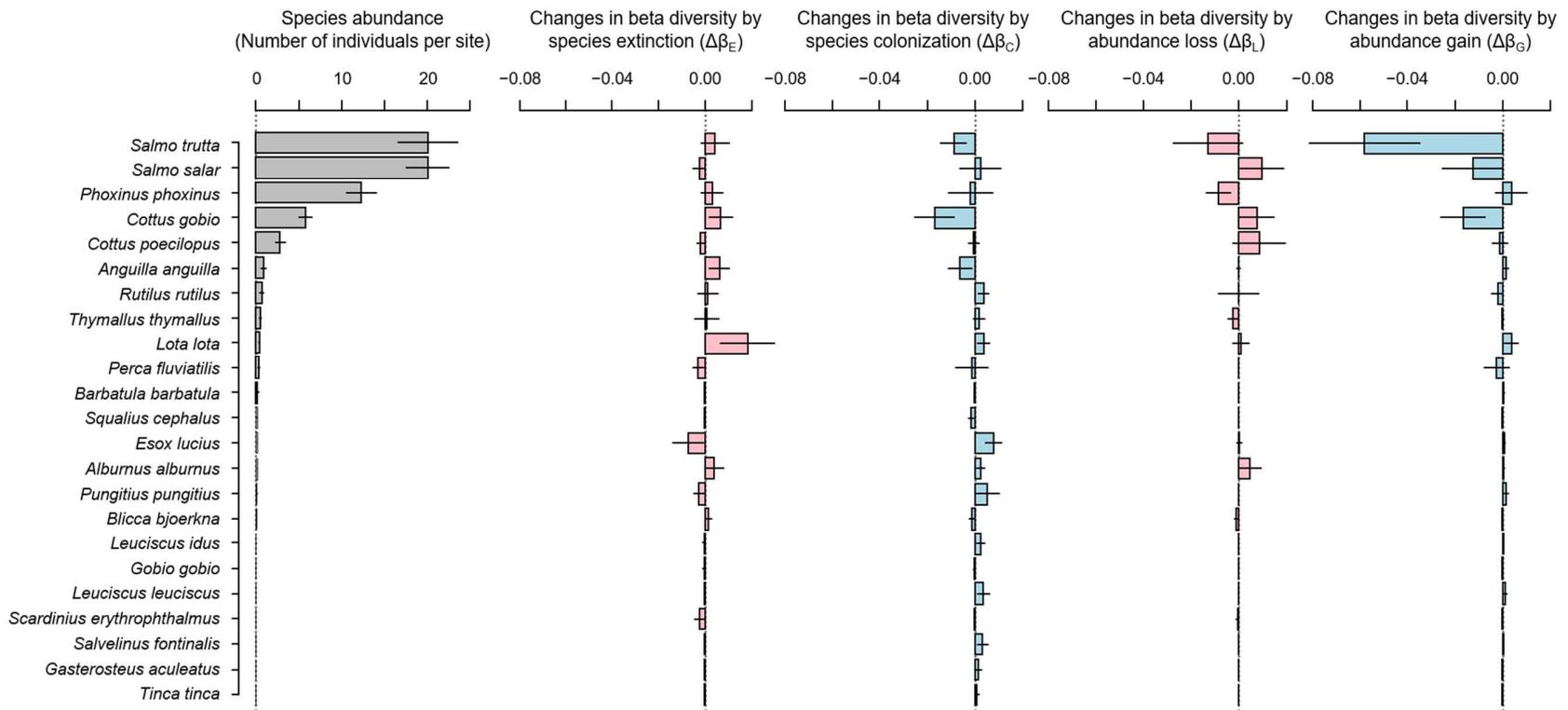


Figure S6. Species abundance and the beta-diversity components of riverine fish communities in 65 waterbodies across Sweden between 1990 and 2018. Beta diversity was defined as the compositional variation among multiple sampling sites within each waterbody. The red and blue bars indicate the impacts of local extinctions and colonizations (i.e., changes from presence to absence and vice versa) and abundance losses and gains on beta diversity. Bars and lines show the means \pm standard errors.