Research article

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

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ABSTRACT

1. Beta diversity, the spatial variation in species composition, is an essential facet of biodiversity. Ecologists have long recognized that the losses and gains in local species abundances can either decrease or increase beta diversity, phenomena often referred to as biotic homogenization and differentiation, respectively. However, quantifying such dynamic impacts of species abundances on beta diversity has remained a methodological challenge.
2. Here, we develop a numerical method to additively partition the temporal changes in beta diversity into distinct components that reflect the losses and gains in local species abundances. Our method is based on Ružička and Bray–Curtis indices and the normalized abundance-based Whittaker's beta diversity. The temporal changes in these measures are partitioned into components that represent biotic homogenization and differentiation driven by abundance losses and gains at both species and community levels.
3. Application of the method to a Swedish fish community dataset revealed decreases in beta diversity between 1990 and 2018. The homogenization of fish communities was explained by gains, but not losses, in species abundances across sites. Species-level partitioning further showed that the homogenization was largely caused by the increased population sizes of brown trout (*Salmo trutta*) in sites where it was already present but in low abundances, resulting in a more spatially-uniform abundance distribution.
4. The results highlight that our partitioning method effectively identifies local population and community processes embedded in regional biodiversity patterns. We believe that explicit analyses of the losses and gains in species abundances should bring deeper insights into the dynamics of beta diversity.

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

1 | INTRODUCTION

Measures of beta diversity, the variation in species composition among sites, play a central role in determining the spatial structure of biodiversity (Whittaker, 1960; Anderson et al., 2011; Legendre & Legendre, 2012; Chao & Chiu, 2016). Among the features that characterize the different measures of beta diversity, one that is critically important is whether a given measure is incidence-based (i.e., presence–absence) or abundance-based (Chao, Chazdon, & Shen, 2005; Legendre & Legendre, 2012; Baselga, 2013). Incidence- and abundance-based measures weigh rare and dominant species differently and thereby provide complementary insights into community structure (Anderson et al., 2011; Legendre & Legendre, 2012; Li et al., 2016). Specifically, abundance-based measures are capable of detecting changes in species dominance patterns without richness differences (Dornelas et al., 2014; Jones, Ripplinger, & Collins, 2017) and are relatively robust against undersampling (Chao et al., 2005, 2014; Barwell, Isaac, & Kunin, 2015). As such, extensions of existing incidence-based methods of beta diversity to incorporate species abundance can allow us to gain a more comprehensive understanding of spatial community structure (Baselga, 2013; Chao et al., 2014).

By using incidence-based measures, previous studies developed numerical methods to disentangle the species extinction and colonization processes that shape beta diversity (Baeten et al., 2014; Rosenblad & Sax, 2017; Tatsumi, Strengbom, Čugunovs, & Kouki, 2020; Tatsumi, Iritani, & Cadotte, 2021). Temporal decreases and increases in beta diversity, termed biotic homogenization and differentiation, respectively, can occur either from species extinctions or colonizations (McKinney & Lockwood, 1999; Olden & Poff, 2003; Socolar, Gilroy, Kunin, & Edwards, 2016; Rosenblad & Sax, 2017; Tatsumi et al., 2020). 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). In our previous study (Tatsumi et al., 2021), we proposed a numerical method to additively partition such impacts of extinctions and colonizations on spatial beta diversity as quantified by incidence-based measures, namely Jaccard and Sørensen indices and Whittaker's beta.

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 across space (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), providing a unified approach for incidence- and abundance-based beta diversity.

2 | METHODS

2.1 | Pairwise dissimilarity

We first describe the additive partitioning of temporal changes in pairwise dissimilarity measures, namely using the Ružička ($\beta_{Ruž}$) and Bray–Curtis indices (β_{BC}) (Bray & Curtis,

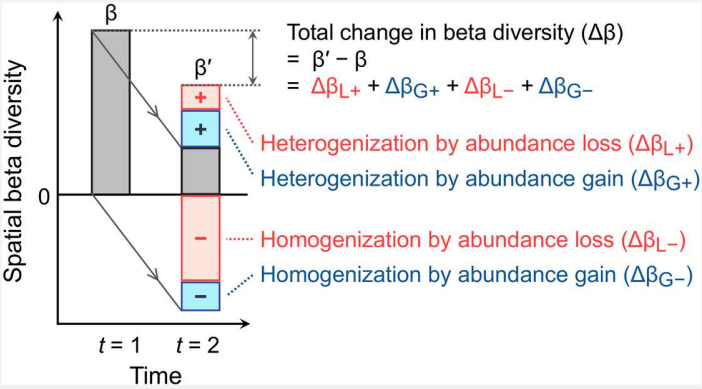


Figure 1. Temporal change in spatial beta diversity and its additive components that represent biotic homogenization and differentiation driven by losses or gains in species abundances.

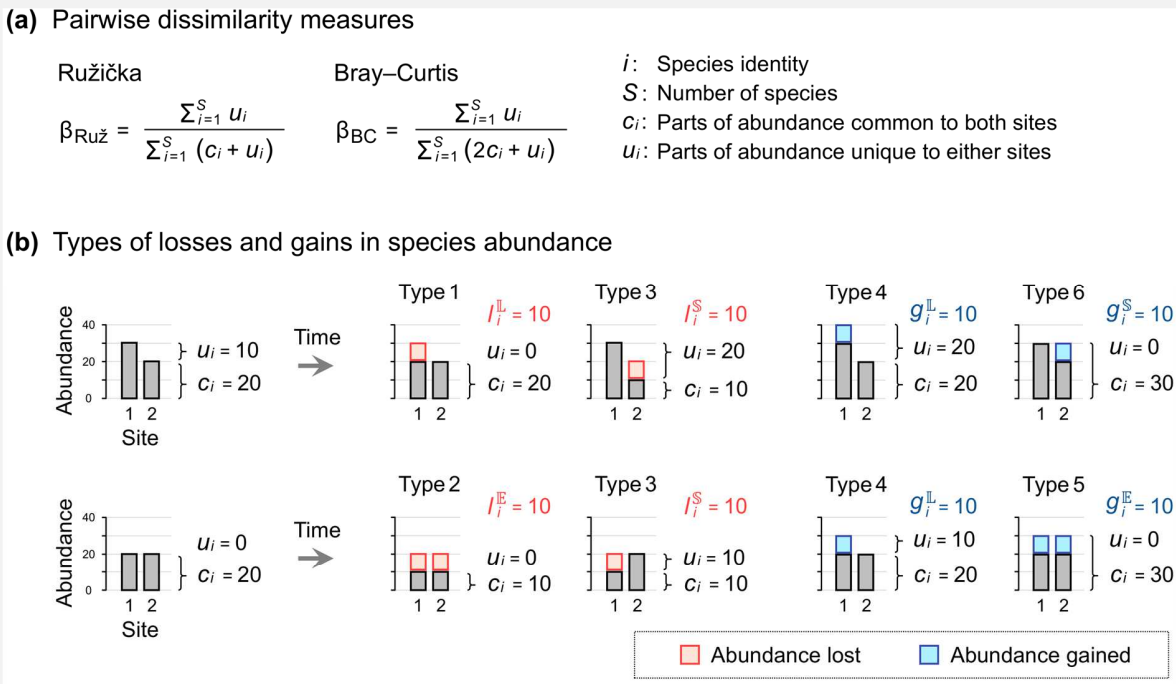
1957; Ružička, 1958) (Figure 2). These measures are defined as $\beta_{\text{Ruž}} = \sum_{i=1}^{S} u_i / \sum_{i=1}^{S} (c_i + u_i)$ and $\beta_{\text{BC}} = \sum_{i=1}^{S} u_i / \sum_{i=1}^{S} (2c_i + u_i)$, where c_i is the component of species abundance common to both sites, u_i is the component of species abundance unique to either site, i is species identity, and S is the number of species. Here, let $\beta_\lambda = \sum_{i=1}^{S} u_i / \sum_{i=1}^{S} (\lambda c_i + u_i)$, then $\beta_{\text{Ruž}} = \beta_1$ and $\beta_{\text{BC}} = \beta_2$. Ružička and Bray–Curtis indices are abundance-extensions of Jaccard and Sørensen indices, respectively, for which the partitioning methods have already been described (Tatsumi et al., 2021).

Previous studies defined six types of species extinctions and colonizations (i.e., changes in presence–absence status) based on their impacts on spatial dissimilarity (Rosenblad & Sax, 2017; Tatsumi et al., 2020, 2021). We here extend these definitions to account for species abundances (Figure 2). The first type is the 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 component that was unique to either site (u_i) at time $t = 1$ becomes lost at time $t = 2$. Type 2 is the case where a component of a_{ik} that was common to both sites (c_i) becomes lost by an equal amount in both sites. Type 3 refers to the loss in c_i in the site where a_{ik} was smaller than, or equal 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 larger than, or equal to, that in the other site. Type 5 is the case where c_i increases by an equal amount in both sites. Type 6 refers to the gain in c_i in the site where a_{ik} was smaller than the other site, turning u_i into c_i. Types 1, 5, and 6 decrease β_λ, leading to homogenization, whereas types 2, 3, and 4 increase β_λ, leading to differentiation. We write $l_i^{\mathbb{L}}$, $l_i^{\mathbb{E}}$, $l_i^{\mathbb{S}}$, $g_i^{\mathbb{L}}$, $g_i^{\mathbb{E}}$, and $g_i^{\mathbb{S}}$ for the amount of changes in abundance that correspond to types 1, 2, 3, 4, 5, and 6, respectively (Figure 2).

It is possible for the abundance of a given species i to change differently in the two sites within the same time interval. Namely, if the abundance a_{ik} decreases in one site (e.g., $k = 1$) where it was larger and increases in the other site (e.g., $k = 2$) where it was smaller, then beta diversity can potentially show no net change (Figure S1). We refer to such offsetting replacements in species abundances as hidden dynamics (Tatsumi et al. 2021). We write d_i for the changes in abundance that fall under this definition. In our partitioning method, we

explicitly describe d_i as a distinct form of abundance losses and gains. In total, there are 32 possible ways a_{ik} can decrease and/or increase, including the hidden dynamics (Figure S1). Further, beta diversity can be much more dynamic than any index portrays since abundances can change multiple times and in multiple ways between sampling intervals, and so here c_i and u_i refer to the net change between $t = 1$ and 2.

For brevity, we write the sum of a given variable across all species (1, 2, ..., S) by using



(c) Consequences of abundance losses and gains on dissimilarity

Type	Description	Temporal changes in … c_i	u_i	$\beta_{Ruž}$ and β_{BC}
1	Decrease in abundance (a_i) in the site where a_i was larger ($\mathbb{L}$) than that in the other site.	0	$-l_i^{\mathbb{L}}$	−
2	Decrease in a_i by equal amount ($\mathbb{E}$) in both sites.	$-l_i^{\mathbb{E}}$	0	+
3	Decrease in a_i in the site where a_i was smaller ($\mathbb{S}$) than, or equal to, that in the other site.	$-l_i^{\mathbb{S}}$	$+l_i^{\mathbb{S}}$	+
4	Increase in a_i in the site where a_i was larger ($\mathbb{L}$) than, or equal to, that in the other site.	0	$+g_i^{\mathbb{L}}$	+
5	Increase in a_i by equal amount ($\mathbb{E}$) in both sites.	$+g_i^{\mathbb{E}}$	0	−
6	Increase in a_i in the site where a_i was smaller ($\mathbb{S}$) than that in the other site.	$+g_i^{\mathbb{S}}$	$-g_i^{\mathbb{S}}$	−

Figure 2. 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.

the uppercase letters (e.g., $\sum_{i=1}^{S} u_i = U$, $\sum_{i=1}^{S} d_i = D$, and $\sum_{i=1}^{S} l_i^{\mathbb{L}} = L^{\mathbb{L}}$). The temporal changes in C and U can then be written as $\Delta C = C' - C = -L^{\mathbb{E}} - L^{\mathbb{S}} + G^{\mathbb{E}} + G^{\mathbb{S}}$ and $\Delta U = U' - U = -L^{\mathbb{L}} + L^{\mathbb{S}} + G^{\mathbb{L}} - G^{\mathbb{S}}$. We can additively partition the temporal changes in pairwise dissimilarity ($\Delta\beta_\lambda = \beta'_{\text{Ruž}} - \beta_{\text{Ruž}}$ when $\lambda = 1$ and $\Delta\beta_\lambda = \beta'_{\text{BC}} - \beta_{\text{BC}}$ when $\lambda = 2$) into six terms that correspond to the six types of abundance changes (see Appendix S1 for the derivation):

$$
\begin{aligned}
\Delta\beta_\lambda &= \beta'_\lambda - \beta_\lambda \\
&= \underbrace{-\frac{p}{U}(L^{\mathbb{L}} + D)}_{\Delta\beta_{\text{L1}}} + \underbrace{\frac{p}{C}L^{\mathbb{E}}}_{\Delta\beta_{\text{L2}}} + \underbrace{\left(\frac{p}{U} + \frac{p}{C}\right)L^{\mathbb{S}}}_{\Delta\beta_{\text{L3}}} \\
&\quad + \underbrace{\frac{p}{U}(G^{\mathbb{L}} + D)}_{\Delta\beta_{\text{G1}}} + \underbrace{\frac{-p}{C}G^{\mathbb{E}}}_{\Delta\beta_{\text{G2}}} + \underbrace{\left(-\frac{p}{U} - \frac{p}{C}\right)G^{\mathbb{S}}}_{\Delta\beta_{\text{G3}}}
\end{aligned}
\tag{1}
$$

where $p = \frac{\lambda CU}{(\lambda C + U)(\lambda C' + U')}$ and C and U are both non-zero.

The variable D denotes the hidden dynamics. The quantities $-\frac{p}{U}D$ in $\Delta\beta_{\text{L1}}$ and $-\frac{p}{U}D$ in $\Delta\beta_{\text{G1}}$ cancel each other out by summing up to zero. These two quantities thus allow us, without causing any effect on $\Delta\beta$, to explicitly account for D in a manner comparable to $-\frac{p}{U}L^{\mathbb{L}}$ and $-\frac{p}{U}G^{\mathbb{L}}$.

The first three terms and the last three terms in Equation 1 are associated with abundance losses and gains, respectively. The first term, which is always negative, represents homogenization by abundance losses ($\Delta\beta_{\text{L}-}$). The second and third terms, which are always positive, indicate differentiation by abundance losses ($\Delta\beta_{\text{L}+}$). Similarly, the fourth term represents differentiation by abundance gains ($\Delta\beta_{\text{G}+}$) and the fifth and sixth terms indicate homogenization by abundance gains ($\Delta\beta_{\text{G}-}$). Depending on the ecological question at hand, one can sum the terms as $\Delta\beta_{\text{L}} = \Delta\beta_{\text{L}-} + \Delta\beta_{\text{L}+}$ and $\Delta\beta_{\text{G}} = \Delta\beta_{\text{G}-} + \Delta\beta_{\text{G}+}$ to assess the total impact of abundance losses and gains on $\Delta\beta$, respectively (Figure 1).

2.2 | Multiple-site variation

Our partitioning approach is applicable to multiple-site measures as well. For cases with

more than two sites, averaging pairwise dissimilarities ($\beta_{\text{Ruž}}$ 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 Whittaker's beta (Harrison, Ross, & Lawton, 1992), defined as $(\gamma/\bar{\alpha} - 1)/(N - 1)$, 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. The extended measure, denoted as β_{Bas} (Baselga's beta), is given by:

$$\beta_{\text{Bas}} = \frac{N \cdot \sum_{i=1}^{S} \max_k\{a_{ik}\} - A}{(N-1)A} \tag{2}$$

where a_{ik} is the abundance of species i in site k, N is the number of sites, S is the number of species, $\max_k\{a_{ik}\}$ is the maximum abundance of species i across all sites, and A is the total abundance of all species in all sites (i.e., $A = \sum_{i=1}^{S} \sum_{k=1}^{N} a_{ik}$). For brevity, we write $\max_k\{a_{ik}\}$ as m_i and $\sum_{i=1}^{S} \max_k\{a_{ik}\}$ as M. We also write the abundance of species i summed across all sites ($\sum_{k=1}^{N} a_{ik}$) as a_{i+}. Note that β_{Bas} is numerically identical to β_{BC} when $N = 2$ (Baselga, 2017) (see Appendix S1).

We extend the variables $l_i^{\mathbb{L}}$, $l_i^{\mathbb{E}}$, $l_i^{\mathbb{S}}$, $g_i^{\mathbb{L}}$, $g_i^{\mathbb{E}}$, and $g_i^{\mathbb{S}}$, defined above (Figure 2), to denote the temporal changes in the maximum abundance (m_i) and the total abundance (a_{i+}) of species i. First, we extend $l_i^{\mathbb{L}}$ to denote the decrease in species abundance associated with both m_i and a_{i+}. This type of abundance loss decreases m_i by $l_i^{\mathbb{L}}$. For example, m_i decreases by 10 when $l_i^{\mathbb{L}} = 10$. 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 $l_i^{\mathbb{L}}$, such that $l_{in}^{\mathbb{L}}$ denotes the decrease in the maximum abundance across n sites. This type of abundance loss decreases a_{i+} by $n \cdot l_{in}^{\mathbb{L}}$. For instance, a_{i+} decreases by 10 when $l_{i1}^{\mathbb{L}} = 10$ and decreases by 20 when $l_{i2}^{\mathbb{L}} = 10$,

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

We extend the definition of $l_i^{\mathbb{E}}$ 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 $l_i^{\mathbb{E}}$ and $N \cdot l_i^{\mathbb{E}}$, respectively. Thus, $l_i^{\mathbb{E}}$ can be seen as a special case of $l_{in}^{\mathbb{L}}$ when $n = N$. We therefore rewrite $l_i^{\mathbb{E}}$ as $l_{iN}^{\mathbb{L}}$ hereafter. Similarly, we rewrite $g_i^{\mathbb{E}}$ as $g_{iN}^{\mathbb{L}}$ for the gain in abundance across all sites in which a given species i showed its maximum abundance at $t = 2$.

We define $l_i^{\mathbb{S}}$ as the abundance loss associated with the decrease in a_{i+} but not m_i. We use the subscript n to let $l_{in}^{\mathbb{S}}$ 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 $n \cdot l_{in}^{\mathbb{S}}$ but does not alter m_i. Similarly, we define $g_{in}^{\mathbb{S}}$ 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 ($N \geq 3$). 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_{ivw} for the abundance losses in v-number of sites and the offsetting gains in w-number of sites occurring within the same time interval ($v \geq 1$, $w \geq 1$, and $v + w \leq N$).

Again, for brevity, we write the sum of a given variable across all species (1, 2, ..., S) using the uppercase letters (e.g., $\sum_{i=1}^{S} \max_k\{a_{ik}\} = \sum_{i=1}^{S} m_i = M$, $\sum_{i=1}^{S} l_{in}^{\mathbb{L}} = L_n^{\mathbb{L}}$, and $\sum_{i=1}^{S} d_{ivw} = D_{vw}$). Equation 1 can be rewritten using the extended definitions by replacing $L^{\mathbb{L}}$, $L^{\mathbb{E}}$, $L^{\mathbb{S}}$, $G^{\mathbb{L}}$, $G^{\mathbb{E}}$, $G^{\mathbb{S}}$, and D with $L_1^{\mathbb{L}}$, $L_2^{\mathbb{L}}$, $L_1^{\mathbb{S}}$, $G_1^{\mathbb{L}}$, $G_2^{\mathbb{L}}$, $G_1^{\mathbb{S}}$, and D_{11}, respectively.

To partition $\Delta\beta_{\mathrm{Bas}}$, we first consider the case of two communities ($N = 2$). The temporal changes in A and M can be written as $\Delta A = A' - A = -L_1^{\mathbb{L}} - 2L_2^{\mathbb{L}} - L_1^{\mathbb{S}} + G_1^{\mathbb{L}} + 2G_2^{\mathbb{L}} + G_1^{\mathbb{S}}$ and $\Delta M = M' - M = -L_1^{\mathbb{L}} - L_2^{\mathbb{L}} + G_1^{\mathbb{L}} + G_2^{\mathbb{L}}$. We can additively partition the temporal changes in $\Delta\beta_{\mathrm{Bas}}$ into six terms that correspond to the six types of abundance changes (see Appendix S1

for the derivation):

$$
\begin{aligned}
\Delta\beta_{\mathrm{Bas}} &= \beta'_{\mathrm{Bas}} - \beta_{\mathrm{Bas}} \\
&= \underbrace{\left(\frac{-q}{M} + \frac{q}{A}\right)(L_1^{\mathbb{L}} + D_{11})}_{\Delta\beta_{\mathrm{L1}}} + \underbrace{\left(\frac{-q}{M} + \frac{2q}{A}\right)L_2^{\mathbb{L}}}_{\Delta\beta_{\mathrm{L2}}} + \underbrace{\frac{q}{A}L_1^{\mathbb{S}}}_{\Delta\beta_{\mathrm{L3}}} \\
&\quad + \underbrace{\left(\frac{q}{M} - \frac{q}{A}\right)(G_1^{\mathbb{L}} + D_{11})}_{\Delta\beta_{\mathrm{G1}}} + \underbrace{\left(\frac{q}{M} - \frac{2q}{A}\right)G_2^{\mathbb{L}}}_{\Delta\beta_{\mathrm{G2}}} + \underbrace{\frac{-q}{A}G_1^{\mathbb{S}}}_{\Delta\beta_{\mathrm{G3}}}
\end{aligned}
\tag{3}
$$

where $q = \frac{NM}{(N-1)A'}$. We define the six terms in Equation 3 as the loss and gain components of temporal changes in multiple-site dissimilarity (β_{Bas}) at $N = 2$. Note that the six terms in Equation 3 are numerically identical to those in Equation 1 when $\lambda = 2$ (i.e., β_{BC}) (see Appendix S1).

Let us now expand the β_{Bas}-based additive partitioning to the case with three sites ($N = 3$), which reads (see Appendix S1 for the derivation):

$$
\begin{aligned}
\Delta\beta_{\mathrm{Bas}} &= \beta'_{\mathrm{Bas}} - \beta_{\mathrm{Bas}} \\
&= \underbrace{\left(\frac{-q}{M} + \frac{q}{A}\right)(L_1^{\mathbb{L}} + D_{11} + D_{12})}_{\Delta\beta_{\mathrm{L-}}} + \underbrace{\left(\frac{-q}{M} + \frac{2q}{A}\right)(L_2^{\mathbb{L}} + D_{21})}_{\Delta\beta_{\mathrm{L-}}\text{ or }\Delta\beta_{\mathrm{L+}}} \\
&\quad + \underbrace{\left(\frac{-q}{M} + \frac{3q}{A}\right)L_3^{\mathbb{L}} + \frac{q}{A}L_1^{\mathbb{S}} + \frac{2q}{A}L_2^{\mathbb{S}}}_{\Delta\beta_{\mathrm{L+}}} \\
&\quad + \underbrace{\left(\frac{q}{M} - \frac{q}{A}\right)(G_1^{\mathbb{L}} + D_{11} + D_{21})}_{\Delta\beta_{\mathrm{G+}}} + \underbrace{\left(\frac{q}{M} - \frac{2q}{A}\right)(G_2^{\mathbb{L}} + hD_{12})}_{\Delta\beta_{\mathrm{G-}}\text{ or }\Delta\beta_{\mathrm{G+}}} \\
&\quad + \underbrace{\left(\frac{q}{M} - \frac{3q}{A}\right)G_3^{\mathbb{L}} + \frac{-q}{A}G_1^{\mathbb{S}} + \frac{-2q}{A}G_2^{\mathbb{S}}}_{\Delta\beta_{\mathrm{G-}}}
\end{aligned}
\tag{4}
$$

Here, the terms are no longer categorized *a priori* into $\Delta\beta_{\mathrm{L1}}$, $\Delta\beta_{\mathrm{L2}}$, $\Delta\beta_{\mathrm{L3}}$, $\Delta\beta_{\mathrm{G1}}$, $\Delta\beta_{\mathrm{G2}}$, and $\Delta\beta_{\mathrm{G3}}$. 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 in Equation 4 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). On the other hand, $\left(\frac{-q}{M}+\frac{2q}{A}\right)L_2^{\mathbb{L}}$ 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.

Following Equations 3 and 4, the temporal changes in $\Delta\beta_{\mathrm{Bas}}$ for N sites can be partitioned as follows (see Appendix S1 for the derivation):

$$
\begin{aligned}
\Delta\beta_{\mathrm{Bas}} &= \beta'_{\mathrm{Bas}} - \beta_{\mathrm{Bas}} \\
&= \underbrace{\sum_{n=1}^{N}\left(\frac{-q}{M}+\frac{nq}{A}\right)L_n^{\mathbb{L}} + \sum_{\{v,w|v+w\le N\}}\left(\frac{-q}{M}+\frac{vq}{A}\right)D_{vw}}_{\Delta\beta_{L-}\text{ or }\Delta\beta_{L+}} + \underbrace{\sum_{n=1}^{N-1}\frac{nq}{A}L_n^{\mathbb{S}}}_{\Delta\beta_{L+}} \\
&\quad + \underbrace{\sum_{n=1}^{N}\left(\frac{q}{M}-\frac{nq}{A}\right)G_n^{\mathbb{L}} + \sum_{\{v,w|v+w\le N\}}\left(\frac{q}{M}-\frac{wq}{A}\right)D_{vw}}_{\Delta\beta_{G-}\text{ or }\Delta\beta_{G+}} + \underbrace{\sum_{n=1}^{N-1}\frac{-nq}{A}G_n^{\mathbb{S}}}_{\Delta\beta_{G-}}
\end{aligned}
\tag{5}
$$

The terms $\Delta\beta_{L-}$ and $\Delta\beta_{L+}$ indicate homogenization and differentiation, respectively, caused by abundance losses. Similarly, $\Delta\beta_{G-}$ and $\Delta\beta_{G+}$ represent homogenization and differentiation, respectively, caused by abundance gains. 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 abundance losses and gains ($L^{\mathbb{L}}$, $L^{\mathbb{E}}$, $L^{\mathbb{S}}$, $G^{\mathbb{L}}$, $G^{\mathbb{E}}$, $G^{\mathbb{S}}$, and D).

2.3 | Species-level impacts on beta diversity

We can further use the partitioning equations to quantify the response of beta diversity to the losses and gains in the abundance of each species independently. For example, consider a case where the abundance of a species that existed in one site was completely lost (i.e., the species went locally extinct). This loss will add $-\frac{p}{U}L^{\mathbb{L}}$ or $\left(\frac{-q}{M}+\frac{q}{A}\right)L_1^{\mathbb{L}}$ to $\Delta\beta$ (see Equations 1 and 5). Thus, the added values can be interpreted as the consequence of the focal species' abundance loss on beta diversity. In this way, $\Delta\beta$ can be additively partitioned into components that reflect the decreases and increases in the population size of individual species. Note that it is possible for a given species to decrease its population size in some sites but increase in other sites within the same time interval, generating both the loss and gain components (i.e., $\Delta\beta_{L-}$, $\Delta\beta_{L+}$, $\Delta\beta_{G-}$, and $\Delta\beta_{G+}$).

3 | APPLICATIONS

We applied the partitioning method to riverine fish community data retrieved from the Swedish Electrofishing Register database (Sers, 2013) via RivFishTIME (Comte et al., 2021). We used data collected in 65 waterbodies consisting a total of 181 permanent sampling sites (2–10 sites per waterbody) across Sweden in 1990 and 2018 (see Appendix S3 for site IDs and selection criteria). The abundance of each fish species in each site was recorded as the number of individuals per 100 m^2. We quantified the compositional variation among sites within each waterbody based on Baselga's beta (β_{Bas}) using either incidence (presence–absence) or abundance data. The incidence data was obtained by transforming the abundance values larger than zero to one. We calculated the temporal changes in beta diversity ($\Delta\beta$) and their additive components between 1990 and 2018. The components representing species extinctions and colonizations (i.e., changes from presence to absence

and vice versa) are denoted as $\Delta\beta_E$ and $\Delta\beta_C$. Those that represent abundance losses and gains are denoted as $\Delta\beta_L$ and $\Delta\beta_G$.

We found that the incidence- and abundance-based approaches provide complementary insights into the changes in beta diversity (Figure 3). While the incidence-based beta diversity showed no temporal trend (Figure 3a), the abundance-based beta diversity significantly decreased from 1990 and 2018, as indicated by $\Delta\beta$ less than zero (Figure 3b). The loss and gain components ($\Delta\beta_L$ and $\Delta\beta_G$) revealed that this homogenization of fish communities was explained by gains, but not losses, in species abundances (Figure 3b). Partitioning $\Delta\beta$ into species-level components further showed that the homogenization was largely caused by brown trout (*Salmo trutta*) (Figure 3d; see Appendix 3 for the results of all species). The fact that the colonization component $\Delta\beta_C$ of brown trout was not significant (Figure 3c) indicates that the homogenization did not result from colonizations of brown trout to new sites. Rather, it was caused by the increased sizes of brown trout populations (potentially associated with fishing restrictions and stocking; Almesjö & Limén, 2009) in sites where they were already present but in low abundances, leading to a more spatially-uniform abundance distribution. Overall, our results highlight that the incidence- and abundance-based components ($\Delta\beta_E$, $\Delta\beta_C$, $\Delta\beta_L$, and $\Delta\beta_G$) collectively revealed spatiotemporal community dynamics that were otherwise undetectable.

4 | CONCLUSIONS

We developed a new method to partition the temporal changes in beta diversity into distinct components that reflect the losses and gains in species abundances (Figure 1). The method provides a unified approach for both incidence and abundance data to obtain a more mechanistic understanding of biotic homogenization and differentiation. By applying the method to an empirical dataset, we identified population and community dynamics that underlie the changes in beta diversity (Figure 3). The capability of our method to quantify species-level processes could help conservation practitioners to assess the impacts of specific

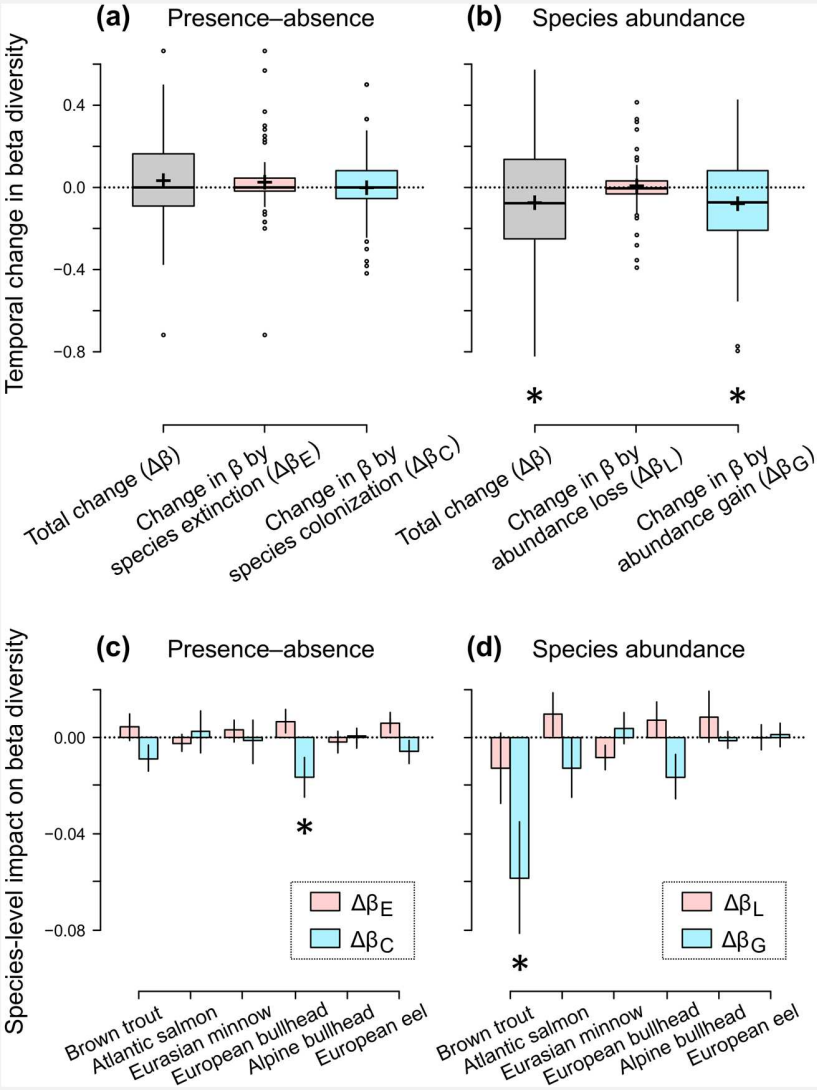


Figure 3. Temporal change in beta diversity and its components of riverine fish communities in 65 waterbodies across Sweden between 1990 and 2018. Beta diversity was defined as the compositional variation among multiple sampling sites within each waterbody. (a) Temporal changes in beta diversity based 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×IQR), respectively. In the bottom panels, bars and lines show the means ± standard errors. Asterisks indicate that the mean value was significantly different from zero (one-sample *t*-test; $P < 0.05$).

species (e.g., increased abundance of an invasive exotic species and decreases in endangered species) on regional biodiversity. Future works require determining how the empirical estimates of the components link to metacommunity theory and regional species coexistence. We believe that explicit analyses of the losses and gains in species abundances should bring deeper insights into ecological community structure across space and time.

AUTHORS' CONTRIBUTIONS

ST conceived the study, derived the partitioning equations, and analyzed the data. ST wrote the manuscript with inputs from RI and MWC.

DATA ACCESSIBILITY

The R scripts for partitioning beta diversity ('ecopart.R'; Ecological COmmunity PARTitioning or Extinction and COlonization PARTitioning) and for extracting the Swedish fish community data from RivFishTIME (Comte et al., 2021) are available at GitHub (https://github.com/communityecologist/ecopart).

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REFERENCES

Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., ... Swenson, N. G. (2011). Navigating the multiple meanings of beta diversity: A roadmap for the practicing ecologist. *Ecology Letters*, *14*, 19–28.

Baeten, L., Warton, D. I., Van Calster, H., De Frenne, P., Verstraeten, G., Bonte, D., ...

Verheyen, K. (2014). A model-based approach to studying changes in compositional heterogeneity. *Methods in Ecology and Evolution*, *5*, 156–164.

Barwell, L. J., Isaac, N. J. B., & Kunin, W. E. (2015). Measuring β-diversity with species abundance data. *Journal of Animal Ecology*, *84*, 1112–1122.

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143.

Baselga, A. (2013). Separating the two components of abundance-based dissimilarity: Balanced changes in abundance vs. abundance gradients. *Methods in Ecology and Evolution*, *4*, 552–557.

Baselga, A. (2017). Partitioning abundance-based multiple-site dissimilarity into components: Balanced variation in abundance and abundance gradients. *Methods in Ecology and Evolution*, *8*, 799–808.

Bray, J. R., & Curtis, J. T. (1957). An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, *27*, 325–349.

Chao, A., Chazdon, R. L., & Shen, T. J. (2005). A new statistical approach for assessing similarity of species composition with incidence and abundance data. *Ecology Letters*, *8*, 148–159.

Chao, A., & Chiu, C. H. (2016). Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. *Methods in Ecology and Evolution*, *7*, 919–928.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, *84*, 45–67.

Comte, L., Carvajal-Quintero, J., Tedesco, P. A., Giam, X., Brose, U., Erős, T., ... Olden, J. D. (2021). RivFishTIME: A global database of fish time-series to study global change ecology in riverine systems. *Global Ecology and Biogeography*, *30*, 38–50.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A.

E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*, 296–299.

Harrison, S., Ross, S. J., & Lawton, J. H. (1992). Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology*, *61*, 151–158.

Jones, S. K., Ripplinger, J., & Collins, S. L. (2017). Species reordering, not changes in richness, drives long-term dynamics in grassland communities. *Ecology Letters*, *20*, 1556–1565.

Legendre, P., & Legendre, L. (2012). Numerical Ecology (3rd ed.). Elsevier.

Li, S., Cadotte, M. W., Meiners, S. J., Pu, Z., Fukami, T., & Jiang, L. (2016). Convergence and divergence in a long-term old-field succession: The importance of spatial scale and species abundance. *Ecology Letters*, *19*, 1101–1109.

McKinney, M. L., & Lockwood, J. L. (1999). Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution*, *14*, 450–453.

Olden, J. D., & Poff, N. L. (2003). Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist*, *162*, 442–460.

Rosenblad, K. C., & Sax, D. F. (2017). A new framework for investigating biotic homogenization and exploring future trajectories: Oceanic island plant and bird assemblages as a case study. *Ecography*, *40*, 1040–1049.

Ružička, M. (1958). Anwendung mathematisch-statisticher Methoden in der Geobotanik (synthetische Bearbeitung von Aufnahmen). *Biológia*, *Bratislava*, *13*, 647–661.

Sers, B. (2013). Swedish Electrofishing RegiSter – SERS. Swedish University of Agricultural Sciences (SLU), Department of Aquatic Resources. Retrieved from http://www.slu.se/electrofishingdatabase (December 21, 2021).

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation? *Trends in Ecology & Evolution*, *31*, 67–80.

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.

Tatsumi, S., Strengbom, J., Čugunovs, M., & Kouki, J. (2020). Partitioning the colonization and extinction components of beta diversity across disturbance gradients. *Ecology*, *101*, e03183.

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*, 279–338.