Research article

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

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ABSTRACT

Spatial variation in species composition, or beta diversity, play central roles in gauging the structure of ecological communities. Here, we develop a new numerical method to partition the impacts of abundance losses and gains on the temporal changes in spatial beta diversity. We show that the temporal changes in pairwise dissimilarity measures (Ružička and Bray–Curtis indices) and a multiple-site measure (normalized Whittaker's beta) can be partitioned into six terms that reflect the losses and gains in species abundance. Our new method provides a unified approach to disentangle the temporal dynamics of spatial community structure by means of either incidence- or abundance-based data.

INTRODUCTION

Dissimilarity measures of species composition play central roles in gauging the spatial and temporal structure of biodiversity (Wolda, 1981; Tamás, Podani, & Csontos, 2001; Anderson et al., 2011; Legendre & Legendre, 2012; Chao & Chiu, 2016). Among the properties that characterize different measures of dissimilarity, one of the most significant is whether a given measure is incidence-based (i.e., presence and absence of species) or abundance-based (Chao, Chazdon, & Shen, 2005; Legendre & Legendre, 2012; Baselga, 2013). Incidence- and abundance-based measures weigh rare and dominant species in different ways and thereby provide complementary insights into community structure (Olsgard, Somerfield, & Carr, 1997; Anderson et al., 2011; Legendre & Legendre, 2012; Li et al., 2016). Besides, abundance-based measures are relatively robust against undersampling (Chao et al., 2005, 2014; Barwell, Isaac, & Kunin, 2015) and are capable of detecting changes in species dominance patterns even in the absence of richness differences (Dornelas et al., 2014; Jones, Ripplinger, & Collins, 2017). Extensions of existing incidence-based methods to account for abundance can thus allow us to gain more comprehensive pictures of spatiotemporal variation in species composition (Baselga, 2013; Chao et al., 2014).

Using incidence-based measures, previous studies have developed numerical methods to disentangle the species extinction and colonization processes that drive the compositional dissimilarity across space, or beta diversity (Baeten et al., 2014; Rosenblad & Sax, 2017; Li, Bellard, Hu, & Li, 2019; Tatsumi, Strengbom, Čugunovs, & Kouki, 2020; Tatsumi, Iritani, & Cadotte, 2021). Temporal decreases and increases in beta diversity (i.e., biotic homogenization and heterogenization, respectively) can both occur as a result of species extinctions or colonizations (i.e., changes from presence to absence, or vice versa) (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 heterogenization (Socolar et al., 2016; Rosenblad & Sax, 2017; Tatsumi et al., 2020). Colonizations cause homogenization when new species become widespread or existing species increase their regional dominance, but drive heterogenization when new species colonize only a few sites (Socolar et al., 2016; Rosenblad & Sax, 2017; Tatsumi et al., 2020). In our previous study (Tatsumi et al., 2021), we proposed a method to empirically partition such impacts of extinctions and colonizations on spatial beta diversity as quantified by incidence-based measures.

Here, we develop a new method to partition the impacts of abundance losses and gains on spatial beta diversity by extending the previous incidence-based methods (Rosenblad & Sax, 2017; Li et al., 2019; Tatsumi et al., 2020, 2021). Similar to species extinctions and colonizations (i.e., binary changes between presence and absence), quantitative decreases and increases in local abundance can drive either homogenization or heterogenization across space (Socolar et al., 2016). The new method allows us to partition such temporal changes in spatial variation ($\Delta\beta = \beta^{\circ} - \beta$, where β and β° are the values at t = 1 and 2, respectively) into distinct terms that reflect abundance losses and gains, providing a unified approach for incidence and abundance data. Our method can be applied to community-survey datasets (species × site matrices at t = 1 and 2) with abundance having been recorded in any form, including density, biomass, or the number of individuals, at either absolute or relative scales.

LOSS AND GAIN COMPONENTS OF ABUNDANCE-BASED BETA DIVERSITY

Pairwise dissimilarity

We first describe the partitioning of temporal changes in pairwise dissimilarity measures, namely Ružička ($\beta_{\text{Ruž}}$) and Bray–Curtis indices (β_{BC}) (Bray & Curtis, 1957; Ružička, 1958) (Fig. 1). 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 u_i is the part of abundance unique to either site, c_i is the part of abundance common to both sites, i is species identity, and S is the number of species. Here, let $\beta_p = \{\sum_{i=1}^{S} u_i\}/\{\sum_{i=1}^{S}(pc_i + u_i)\}$, then $\beta_{\text{Ruž}} = \beta_1$ and $\beta_{\text{BC}} = \beta_2$.

Previous studies have 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 abundance (Fig. 1). The first type is the reduction in u_i (type 1 in Fig. 1); that is, for a given species i, a part of abundance unique to either site (u_i) at time t = 1 becomes lost at time t = 2. Type 2 is the case where a part of abundance common to both sites (c_i) becomes lost by equal amount in both sites. Type 3 (or 3′) refers to the loss of c_i in either site where the abundance is smaller than, or equal to, that in the other site, whereby c_i at t = 1 turns into u_i at t = 2. Type 4 (or 4′) refers to the gain of u_i in the site where the abundance is larger than, or equal to, that in the other site. Type 5 is the case where c_i increases by equal amount in both sites. Type 6 refers to the gain of abundance in the site where it was smaller than the other site, whereby u_i turns into c_i. Types 1, 5, and 6 decrease β_p,

(a) Pairwise dissimilarity measures

Ružička

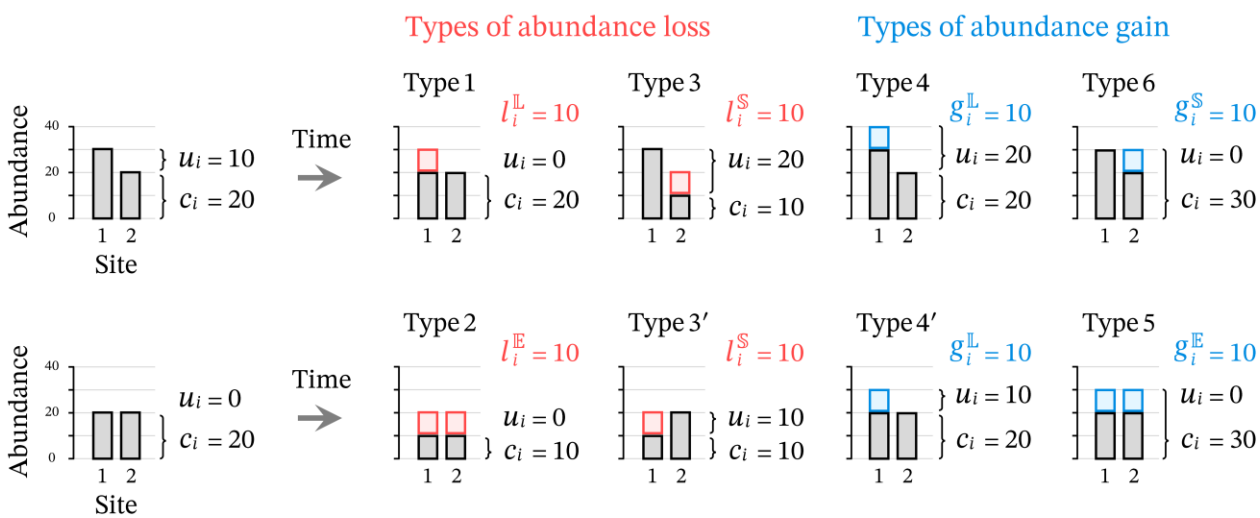
$$\beta_{\text{Ruž}} = \frac{\sum_{i=1}^{S} u_i}{\sum_{i=1}^{S} (c_i + u_i)}$$

Bray–Curtis

$$\beta_{\text{BC}} = \frac{\sum_{i=1}^{S} u_i}{\sum_{i=1}^{S} (2c_i + u_i)}$$

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

(b) Examples of losses and gains in species abundance



(c) Consequences of abundance losses and gains on dissimilarity

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

Figure 1. Schematic representation of the temporal changes in abundance-based beta diversity and its loss and gain components. (a) Ružička and Bray–Curtis dissimilarity indices, (b) examples of abundances losses and gains categorized into six types based on their impacts on dissimilarity, and (c) the description of the six types of abundances losses and gains.

leading to homogenization, whereas types 2, 3, and 4 increase β_p, leading to heterogenization. We denote the amount of changes in abundance that correspond to types 1, 2, 3, 4, 5, and 6 as $l_i^{\mathbb{L}}$, $l_i^{\mathbb{E}}$, $l_i^{\mathbb{S}}$, $g_i^{\mathbb{L}}$, $g_i^{\mathbb{E}}$, and $g_i^{\mathbb{S}}$, respectively (Fig. 1).

It is possible for the abundance of a given species *i* to change differently in the two sites during the same time interval. Namely, if the abundance decreases in the site where it was larger and increases in the other site where it was smaller, then beta diversity can potentially show no net change. We refer to such offsetting replacements in species abundance as "hidden" dynamics (Tatsumi et al. 2021). We denote the changes in abundance that fall under this definition as d_i. In our partitioning method, d_i is explicitly taken into account as a distinct form of abundance losses and gains. In total, there are 24 possible combinations of abundance losses and gains, including the hidden dynamics.

For compact notations, we denote the sum of a given variable across all species (1, 2, …, *S*) using the uppercase letters (e.g., $\sum_i^S u_i = U$ and $\sum_i^S l_i^{\mathbb{L}} = L^{\mathbb{L}}$). To distinguish the variables at *t* = 1 and *t* = 2, we add the superscript ° to the latter (e.g., β_p°). The temporal changes in *U* and *C* can then be described as $\Delta U = U^{\circ} - U = -L^{\mathbb{L}} + L^{\mathbb{S}} + G^{\mathbb{L}} - G^{\mathbb{S}}$ and $\Delta C = C^{\circ} - C = -L^{\mathbb{E}} - L^{\mathbb{S}} + G^{\mathbb{E}} + G^{\mathbb{S}}$ (Fig. 1). The relative changes in *U* and *C* can be defined as $\lambda_U = \Delta U / U$ and $\lambda_C = \Delta C / C$, where *U* and *C* are both non-zero. We can additively partition the temporal changes in pairwise dissimilarity ($\Delta\beta_p = \beta_{\text{Ruž}}^{\circ} - \beta_{\text{Ruž}}$ when *p* =1 and $\Delta\beta_p = \beta_{\text{BC}}^{\circ} - \beta_{\text{BC}}$ when *p* =2) into six terms that correspond to the six types of abundance changes:

$$\begin{aligned}\Delta\beta_p &= \beta_p^{\circ} - \beta_p \\ &= \underbrace{-\frac{x}{U}(L^{\mathbb{L}} + hD)}_{\Delta\beta_1} + \underbrace{\frac{x}{C}L^{\mathbb{E}}}_{\Delta\beta_2} + \underbrace{\left(\frac{x}{C} + \frac{x}{U}\right)(L^{\mathbb{S}} + (1-h)D)}_{\Delta\beta_3} \\ &\quad + \underbrace{\frac{x}{U}(G^{\mathbb{L}} + hD)}_{\Delta\beta_4} + \underbrace{\frac{-x}{C}G^{\mathbb{E}}}_{\Delta\beta_5} + \underbrace{\left(-\frac{x}{C} - \frac{x}{U}\right)(G^{\mathbb{S}} + (1-h)D)}_{\Delta\beta_6}\end{aligned} \tag{Eq. 1}$$

where $x = \frac{\beta_p(1-\beta_p)}{(1-\beta_p)\lambda_C + \beta_p\lambda_U + 1}$ is a scaling factor and *h* is a parameter associated with hidden dynamics (see the second next paragraph for detail).

The first three terms and the last three terms in Eq. 1 represent the subtractive (abundance-loss) components and the additive (abundance-gain) components of $\Delta\beta_p$. The first term is always

negative, whereas the second and third terms are both positive. We therefore refer to the first term as subtractive homogenization ($\Delta\beta_{\mathrm{Loss}-}$) and the sum of second and third terms as subtractive heterogenization ($\Delta\beta_{\mathrm{Loss}+}$). For similar reasons, we refer to the fourth term as additive heterogenization ($\Delta\beta_{\mathrm{Gain}+}$) and the sum of fifth and sixth terms as additive homogenization ($\Delta\beta_{\mathrm{Gain}-}$). Depending on the ecological question at hand, one can sum the terms as $\Delta\beta_{\mathrm{Loss}} = \Delta\beta_{\mathrm{Loss}-} + \Delta\beta_{\mathrm{Loss}+}$ and $\Delta\beta_{\mathrm{Gain}} = \Delta\beta_{\mathrm{Gain}+} + \Delta\beta_{\mathrm{Gain}-}$ to represent the total impacts of abundance losses and gains, respectively (Fig. 1).

The parameter h in Eq. 1 ranges in the interval [0, 1] and determines the balance between two different ways the hidden dynamics can arise. First, the hidden dynamics can arise in such a way that the abundance first decreases in one site and then increases in the other site during a given time interval. That is, the abundance is lost in site 1 before it is gained in site 2. Such abundance losses and gains correspond to the type-1 losses ($l_i^{\mathbb{L}}$) and the type-4′ gains ($g_i^{\mathbb{L}}$), respectively. In Eq. 1, the associated decreases and increases in β_p are taken into account by adding hd_i to $L^{\mathbb{L}}$ and $G^{\mathbb{L}}$ in the first and fourth terms, respectively. The second form of hidden dynamics is where the abundance is gained prior to getting lost. Such gains and losses correspond to the type-5 gains ($g_i^{\mathbb{S}}$) and the type-2′ losses ($l_i^{\mathbb{S}}$), respectively. The resultant decreases and increases in β_p are reflected in Eq.1 by adding $(1-h)d_i$ to $G^{\mathbb{S}}$ and $L^{\mathbb{S}}$ in the sixth and third terms, respectively. As such, the parameter h determines how the order of abundance losses and gains affect $\Delta\beta_p$ via d_i. When h = 0, abundance is always lost before it is gained within a given time interval, and vice versa when h = 1. When h = 0.5, neutrality is assumed with regards to the order of abundance losses and gains.

Multiple-site variation

Our partitioning approach can not only be applied to pairwise measures but also to multiple-site dissimilarity measures. We here consider the normalized Whittaker's beta (Harrison, Ross, & Lawton, 1992) defined as $(\gamma/\overline{\alpha} - 1)/(N-1)$, where γ is the regional species richness, $\overline{\alpha}$ is the mean local species richness, and N is the number of sites. While the original Whittaker's beta ($\gamma/\overline{\alpha}$) 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. We denote the extended measure as β_{HB} (Harrison–Baselga's beta) defined as:

$$\beta_{\mathrm{HB}} = \frac{N \cdot \sum_i^S \max_j\{a_{ij}\} - A}{(N-1)A}$$

(Eq. 2)

where a_{ij} is the abundance of species i in site j, N is the number of sites, S is the number of species, $\max_j\{a_{ij}\}$ is the maximum abundance of species i across all sites, and A is the total abundance of all species in all sites (i.e., $A = \sum_i^S \sum_j^N a_{ij}$). For notational simplicity, we denote $\max_j\{a_{ij}\}$ as m_i and $\sum_i^S \max_j\{a_{ij}\}$ as M. We also denote the abundance of species i summed across the sites ($\sum_j^N a_{ij}$) as a_{i+}.

The variables $l_i^{\mathbb{L}}$, $l_i^{\mathbb{E}}$, $l_i^{\mathbb{S}}$, $g_i^{\mathbb{L}}$, $g_i^{\mathbb{E}}$, and $g_i^{\mathbb{S}}$, which we defined above to describe the changes in u_i and c_i (Fig. 1), can be extended to represent the changes in the maximum abundance (m_i) and the total abundance (a_{i+}) of species i. First, we extend the definition of $l_i^{\mathbb{L}}$, such that it denotes the temporal decreases in abundance associated with both m_i and a_{i+}. This type of abundance loss leads to reductions in m_i by the amount equal to $l_i^{\mathbb{L}}$. For example, m_i decreases by 10 when $l_i^{\mathbb{L}} = 10$. The amount of reduction 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 the subscript n to $l_i^{\mathbb{L}}$, such that $l_{in}^{\mathbb{L}}$ denotes the decreases in the maximum abundance across n sites. Such abundance losses cause reductions in a_{i+} by the amount equal to $nl_{in}^{\mathbb{L}}$. For instance, a_{i+} decreases by 10 and 20 when $l_{i1}^{\mathbb{L}} = 10$ and $l_{i2}^{\mathbb{L}} = 10$, respectively, whereas m_i decreases by 10 in either cases. Similarly, we define $g_{in}^{\mathbb{L}}$ to denote the increases in the maximum abundance of species i across n sites.

The extended definition of $l_i^{\mathbb{E}}$ represents the abundance losses in all sites (N) across which a given specie i showed the same abundance at t = 1. In this case, m_i and a_{i+} decrease by $l_i^{\mathbb{E}}$ and $Nl_i^{\mathbb{E}}$, 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, $g_i^{\mathbb{E}}$ is rewritten as $g_{iN}^{\mathbb{L}}$ to indicate the gains in abundance across all sites that result in a given species i having the same abundance at t = 2.

The extended definition of $l_i^{\mathbb{S}}$ refers to the abundance losses associated with decreases in a_{i+} but not m_i. We use the subscript n to let $l_{in}^{\mathbb{S}}$ denote the abundance losses in n sites across which a given species i showed smaller abundance than, or equal abundance to, m_i at both t = 1 and t = 2. This type of abundance losses lead to a reduction in a_{i+} by $nl_{in}^{\mathbb{S}}$ but do 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 t = 2.

Hidden dynamics can not only occur in cases with two sites (N = 2) but also with multiple sites (N > 2). As such, we extend the definition of hidden dynamics to refer to the abundance losses in 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 p and q to d_i, we write d_{ipq} to denote the abundance losses in p-number of sites and gains in q-number of sites ($p + q \leq N$) occurring within the same time interval.

We denote the variables $l_{in}^{\mathbb{L}}$, $l_{in}^{\mathbb{S}}$ $g_{in}^{\mathbb{L}}$, $g_{in}^{\mathbb{S}}$, and d_{ipq} summed across all species (i = 1, 2, …, S) as $L_n^{\mathbb{L}}$, $L_n^{\mathbb{S}}$, $G_n^{\mathbb{L}}$, $G_n^{\mathbb{S}}$, and D_{pq}, respectively. 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 $\Delta\beta_{\mathrm{HB}}$, we first consider the case of two communities (N = 2). The temporal changes in M and A can be described as $\Delta M = M^{\circ} - M = -L_1^{\mathbb{L}} - L_2^{\mathbb{L}} + G_1^{\mathbb{L}} + G_2^{\mathbb{L}}$ and $\Delta A = A^{\circ} - A = -L_1^{\mathbb{L}} - 2L_2^{\mathbb{L}} - L_1^{\mathbb{S}} + G_1^{\mathbb{L}} + 2G_2^{\mathbb{L}} + G_1^{\mathbb{S}}$. The relative changes in M and A can be defined as $\lambda_M = \Delta M/M$ and $\lambda_A = \Delta A/A$. We can additively partition the temporal changes in $\Delta\beta_{\mathrm{HB}}$ into six terms that correspond to the six types of abundance changes:

$$\begin{aligned}\Delta\beta_{\mathrm{HB}} &= \beta_{\mathrm{HB}}^{\circ} - \beta_{\mathrm{HB}} \\ &= \underbrace{\left(\frac{-y}{M} + \frac{y}{A}\right)(L_1^{\mathbb{L}} + hD_{11})}_{\Delta\beta_1} + \underbrace{\left(\frac{-y}{M} + \frac{2y}{A}\right)L_2^{\mathbb{L}}}_{\Delta\beta_2} + \underbrace{\frac{y}{A}\left(L_1^{\mathbb{S}} + (1-h)D_{11}\right)}_{\Delta\beta_3} \\ &\quad + \underbrace{\left(\frac{y}{M} - \frac{y}{A}\right)(G_1^{\mathbb{L}} + hD_{11})}_{\Delta\beta_4} + \underbrace{\left(\frac{y}{M} - \frac{2y}{A}\right)G_2^{\mathbb{L}}}_{\Delta\beta_5} + \underbrace{\frac{-y}{A}\left(G_1^{\mathbb{S}} + (1-h)D_{11}\right)}_{\Delta\beta_6}\end{aligned} \qquad \text{(Eq. 3)}$$

where $y = \frac{NM}{(N-1)(\lambda_A+1)A}$ is a scaling factor. We define the six terms in Eq. 3 as the loss and gain components of temporal changes in multiple-site dissimilarity (β_{HB}) at N = 2. The definitions of these components are in line with those based on the Ružička ($\beta_{\mathrm{Ruž}}$) Bray–Curtis indices (β_{BC}) (Eq. 1).

Following Eq. 3, the additive partitioning of temporal changes in $\Delta\beta_{\mathrm{HB}}$ for N sites can be generalized as:

$$
\begin{aligned}
\Delta\beta_{\mathrm{HB}} &= \beta_{\mathrm{HB}}^{\circ} - \beta_{\mathrm{HB}} \\
&= \underbrace{\sum_{n=1}^{N}\left(\frac{-y}{M}+\frac{ny}{A}\right)L_n^{\mathbb{L}} + \sum_{\{p,q|p+q\le N\}}\left(\frac{-y}{M}+\frac{py}{A}\right)hD_{pq}}_{\Delta\beta_{\mathrm{Loss-}}\text{ or }\Delta\beta_{\mathrm{Loss+}}} \\
&\quad + \underbrace{\sum_{n}^{N-1}\frac{ny}{A}L_n^{\mathbb{S}} + \sum_{\{p,q|p+q\le N\}}\frac{py}{A}(1-h)D_{pq}}_{\Delta\beta_{\mathrm{Loss+}}} \\
&\quad + \underbrace{\sum_{j=1}^{N}\left(\frac{y}{M}-\frac{ny}{A}\right)G_n^{\mathbb{L}} + \sum_{\{p,q|p+q\le N\}}\left(\frac{y}{M}-\frac{qy}{A}\right)hD_{pq}}_{\Delta\beta_{\mathrm{Gain-}}\text{ or }\Delta\beta_{\mathrm{Gain+}}} \\
&\quad + \underbrace{\sum_{n}^{N-1}\frac{-ny}{A}G_n^{\mathbb{S}} + \sum_{\{p,q|p+q\le N\}}\frac{-qy}{A}(1-h)D_{pq}}_{\Delta\beta_{\mathrm{Gain-}}}
\end{aligned}
\qquad \text{(Eq. 4)}
$$

DISCUSSION

Here, we developed a new method that allows us to partition the temporal changes in beta diversity into distinct terms that reflect abundance losses and gains. The method provides a unified approach to disentangle the dynamics of spatial community structure by means of either incidence or abundance data.

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