METHOD

Temporal changes in spatial variation: partitioning the extinction and colonisation components of beta diversity

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Abstract

The last two decades have witnessed unprecedented changes in beta diversity, the spatial variation in species composition, from local to global scales. However, analytical challenges have hampered empirical ecologists from quantifying the extinction and colonisation processes behind these changing beta diversity patterns. Here, we develop a novel numerical method to additively partition the temporal changes in beta diversity into components that reflect local extinctions and colonisations. By applying this method to empirical datasets, we revealed spatiotemporal community dynamics that were otherwise undetectable. In mature forests, we found that local extinctions resulted in tree communities becoming more spatially heterogeneous, while colonisations simultaneously caused them to homogenise. In coral communities, we detected non-random community disassembly and reassembly following an environmental perturbation, with a temporally varying balance between extinctions and colonisations. Partitioning the dynamic processes that underlie beta diversity can provide more mechanistic insights into the spatiotemporal organisation of biodiversity.

Keywords

Biotic homogenisation, community assembly, metacommunity, spatial heterogeneity, species turnover, temporal ecology.

INTRODUCTION

The dynamics of species diversity across two fundamental axes—space and time—lie at the heart of ecology (Rosenzweig 1995). Ecological theory predicts that the spatial variation in species composition increases over time, even under initially uniform environmental conditions, owing to the cumulative impacts of dispersal, biotic interactions and ecological drift (Chase 2003; Mouquet & Loreau 2003; Fukami 2015). However, recent anthropogenic forces have caused community disassembly and reassembly at unprecedented rates (Kidwell 2015), thereby disrupting the ecological processes that maintain the spatial variation. Empirical studies have shown consequent reductions in spatial community variation across various types of ecosystems (e.g. terrestrial, freshwater and marine) and taxonomic groups (e.g. plants, birds, fish, fungi and bacteria) from local to global scales (McKinney & Lockwood 1999; Olden & Rooney 2006; Barberán *et al.* 2015; Gossner *et al.* 2016; Finderup Nielsen *et al.* 2019). With the accelerating pace and extent of spatiotemporal species dynamics, detailed assessments of community reorganisations have become increasingly important.

Temporal changes in spatial community variation result primarily from extirpations (or local extinctions) and colonisations of species in different sites (Olden & Poff 2003; Olden &

Rooney 2006); here, we use the term extirpation to denote the local loss of a species in a given site. Beta diversity, generally defined as the spatial variation in species composition, provides a connection between the local diversity at a specific site (alpha diversity) and the diversity in the larger region (gamma diversity) (Whittaker 1960; Anderson *et al.* 2011). Beta diversity can either decrease or increase in response to extirpations and colonisations (Olden & Poff 2003; Olden & Rooney 2006; Socolar *et al.* 2016; Tatsumi *et al.* 2020). Specifically, extirpations result in biotic homogenisation (i.e. decreases in beta diversity) when rare, infrequent species become regionally extinct, but can otherwise lead to biotic heterogenisation (i.e. increases in beta diversity). Colonisations cause homogenisation when new species become widespread or species that already exist in the region increase in their frequencies, but can also drive heterogenisation when new species colonise only a few sites (Socolar *et al.* 2016; Tatsumi *et al.* 2020). Explicit considerations of extirpations and colonisations are thus required to gauge their consequences on regional compositional variation. Doing so can also allow us to draw more direct links between spatial processes and patterns associated with metacommunity theory (Leibold & Chase 2017).

In natural communities, the two processes (extirpation and colonisation) and the two contrasting outcomes (homogenisation and heterogenisation) typically occur in concert.

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McKinney & Lockwood (1999), who coined the term biotic homogenisation, stated that "understanding the dynamics of homogenisation will be challenging because it subsumes many complex aspects of the biodiversity crisis such as extinction and species introductions." As this quote makes clear, ecologists have long recognised that species losses and gains *concurrently* drive homogenisation (Vitousek 1997; Olden & Poff 2003; Olden & Rooney 2006; Li *et al.* 2016). It is also important to note that these processes can reinforce or mask one another. For example, disturbance can exclude widespread species, thus increasing heterogeneity, but can simultaneously induce spatially uniform colonisations of new species, thus increasing homogeneity (Tatsumi *et al.* 2020). Such opposing outcomes can lead us to misinterpretations that there has been no driving force responsible for changes in beta diversity. To gain deeper insights into spatial community dynamics, the synchronous extirpation–colonisation processes and the resulting homogenisation and heterogenisation must be disentangled.

Here, we develop a new analytical method to additively partition the net temporal change in beta diversity ($\Delta\beta_{\text{Total}}$) into components that reflect species extirpations and colonisations (Fig. 1). Our study extends previous methodological developments on beta diversity. First, the types of homogenisation and heterogenisation that we use in this study follow the definitions by Olden & Poff (2003) and Rosenblad and Sax (2017). Whereas these previous studies explored the $\Delta\beta_{\text{Total}}$ under given extirpation and colonisation scenarios, we here derive equations that partition the $\Delta\beta_{\text{Total}}$ based on empirical datasets. Our method can also be seen as a spatial extension of Legendre's (2019) formulation of temporal beta diversity. Namely, while Legendre (2019) dealt with the partitioning of the extirpation and colonisation processes within a single community over time, our method partitions the two processes in altering the spatial variation across multiple communities over time. Below, we derive the equations that partition the extirpation and colonisation components. We then conduct sensitivity analyses to verify the model performance and apply the partitioning method to forest and coral reef datasets. Finally, we discuss future applications of the method and implications for biological conservation.

PARTITIONING BETA DIVERSITY INTO DYNAMIC COMPONENTS

Pairwise dissimilarity

We first describe the partitioning of temporal changes in beta diversity based on pairwise dissimilarity metrics (Fig. 2a), namely Jaccard (β_J) and Sørensen indices (β_S). These metrics are defined as $\beta_J = B/(A + B)$ and $\beta_S = B/(2A + B)$, where A is the number of species present in both sites (hereafter "shared species") and B is the number of species unique to either site ("unique species"). Here, let $D_p = B/(pA + B)$, then $\beta_J = D_1$ and $\beta_S = D_2$. Our method assumes community survey data (site × species matrices) collected at two points in time to calculate $\Delta\beta_{\text{Total}}$ ($=\beta' - \beta$, where β and β' are beta diversity at $t = 1$ and $t = 2$ respectively).

Following Rosenblad and Sax (2017), we define six types of extirpation and colonisation processes (i.e. temporal changes in the presence and absence of species) in terms of their effects on D_p (Fig. 2b). The first type refers to extirpations of species unique to either site; that is, species that were present in one of the sites at $t = 1$ become absent at $t = 2$. The second type is extirpations of shared species in both sites. The third is extirpations of shared species in one site, whereby the species become unique to the other site. The fourth is cases where species that were absent in both sites at $t = 1$ colonise one of the sites, and become recorded as unique species at $t = 2$. The fifth is where species that were absent in both sites colonise both sites, and become shared species. The sixth is where species that were unique to either site colonise the other site as well, and become shared species.

The combinations of the six types of extirpation or colonisation cover all possible ways of changes in the numbers of shared
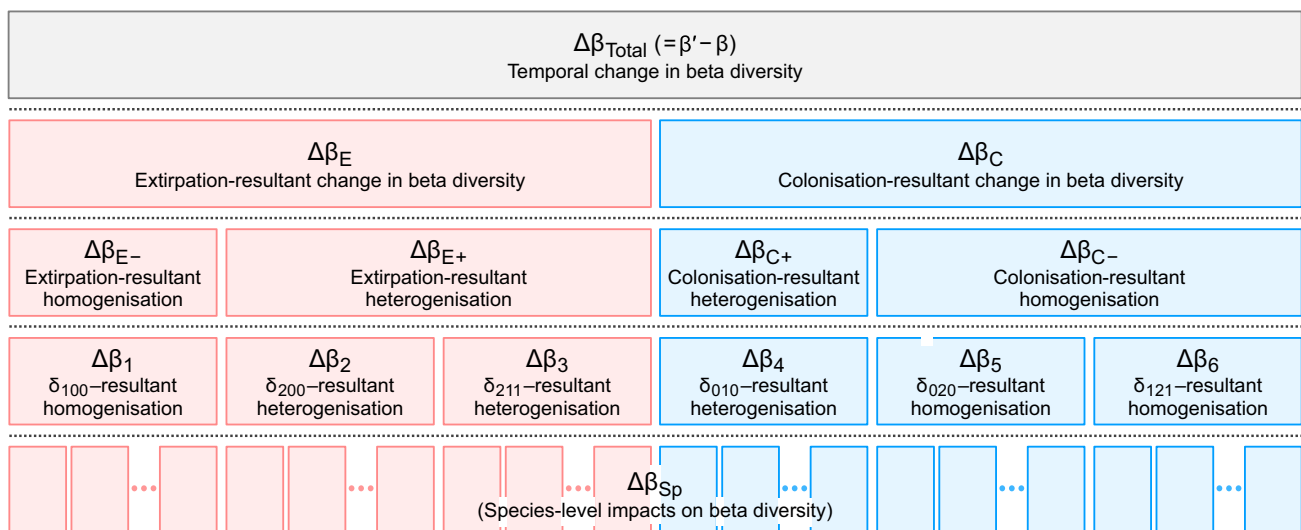
Figure 1 Temporal changes in beta diversity ($\Delta\beta_{\text{Total}}$) and its extirpation and colonisation components. $\Delta\beta_{\text{Total}}$, defined as the difference in beta diversity between times $t = 1$ (β) and $t = 2$ (β'), can be additively partitioned into four components ($\Delta\beta_{E-}$, $\Delta\beta_{E+}$, $\Delta\beta_{C+}$ and $\Delta\beta_{C-}$), six components ($\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$ and $\Delta\beta_6$ in cases with $N = 2$ sites), or a number of components that reflect the dynamics of individual species ($\Delta\beta_{\text{Sp}}$). See Fig. 2 and the main text for the definition of δ_{xyz}. The sum of all components in each row equals $\Delta\beta_{\text{Total}}$.

(a) Temporal changes in beta diversity

Species

$t = 1$ Site 1 | 1 0 | 1 | 1 1 | 0 0 | 0 | 1 0 | 1 0 | 1 0 | 1 |
Site 2 | 0 1 | 1 | 1 1 | 0 0 | 0 | 0 1 | 0 1 | 0 1 | 1 |

Extirpation   Colonisation

| 0 | 0 | 0 | 1 | 1 | 1 0 | 1 |
| 0 0 0 | 1 1 | 1 0 |

$t = 2$ Site 1 | 0 0 | 0 | 1 0 | 1 0 | 1 | 1 1 | 0 1 | 1 0 | 1 |
Site 2 | 0 0 | 0 | 0 1 | 0 1 | 1 | 1 1 | 1 0 | 0 1 | 1 |

Types of change δ_{100} δ_{211} δ_{020} δ_{110} δ_{222}
δ_{200} δ_{010} δ_{121} δ_{111}

Beta diversity (e.g., Sørensen index)

$$\beta = \frac{B}{2A+B} = \frac{\delta_{100}+\delta_{121}+\delta_{110}+\delta_{111}}{\{2(\delta_{200}+\delta_{211}+\delta_{222}) + \delta_{100}+\delta_{121}+\delta_{110}+\delta_{111}\}}$$

$$\beta'-\beta = \Delta\beta_{Total}$$

$$\beta' = \frac{B'}{2A'+B'} = \frac{\delta_{211}+\delta_{010}+\delta_{110}+\delta_{111}}{\{2(\delta_{020}+\delta_{121}+\delta_{222}) + \delta_{211}+\delta_{010}+\delta_{110}+\delta_{111}\}}$$

A : Number of species shared by both communities
B : Number of species unique to either community

(b) Extirpation impacts on beta diversity

Species

$t = 1$ Site 1 | 1 1 1 0 1 1 1 1 |
Site 2 | 0 0 0 1 1 1 1 1 |

Colonisation impacts on beta diversity

Species

$t = 1$ Site 1 | 0 0 0 0 1 1 1 0 |
Site 2 | 0 0 0 0 0 0 0 1 |

		$A'-A$	$B'-B$	$\beta'-\beta$
Type 1: δ_{100}-resultant homogenisation	$t = 2$ 1 | 0 0 0 0 1 1 1 1 | 2 | 0 0 0 0 1 1 1 1 |	0	$-\delta_{100}$	$-$
Type 2: δ_{200}-resultant heterogenisation	$t = 2$ 1 | 1 1 1 0 0 0 0 0 | 2 | 0 0 0 1 0 0 0 0 |	$-\delta_{200}$	0	$+$
Type 3: δ_{211}-resultant heterogenisation	$t = 2$ 1 | 1 1 1 0 1 1 1 0 | 2 | 0 0 0 1 0 0 0 1 |	$-\delta_{211}$	$+\delta_{211}$	$+$
Type 4: δ_{010}-resultant heterogenisation	$t = 2$ 1 | 1 1 1 0 1 1 1 0 | 2 | 0 0 0 1 0 0 0 1 |	0	$+\delta_{010}$	$+$
Type 5: δ_{020}-resultant homogenisation	$t = 2$ 1 | 1 1 1 1 1 1 1 0 | 2 | 1 1 1 1 0 0 0 1 |	$+\delta_{020}$	0	$-$
Type 6: δ_{121}-resultant homogenisation	$t = 2$ 1 | 0 0 0 0 1 1 1 1 | 2 | 0 0 0 0 1 1 1 1 |	$+\delta_{121}$	$-\delta_{121}$	$-$

Figure 2 Schematic representation of (a) temporal changes in beta diversity (i.e. spatial variation in species composition) and (b) effects of species extirpation and colonisation on beta diversity. Examples are shown for cases with two sites ($N = 2$). Prime symbols indicate variables at time $t = 2$ (e.g. β'). Red squares show changes from presence (1) to absence (0) by extirpations between two time points ($t = 1$ and 2). Blue squares indicate changes from absence to presence by colonisation. Variable δ_{xyz} represents the number of species that occurred in x-number of sites at $t = 1$, y-number of sites at $t = 2$ and z-number of sites at both $t = 1$ and 2. The top panel (a) shows nine types which δ_{xyz} can fall into; note that either one or two examples (species) are shown for each type. The first six types (δ_{100}, δ_{200}, δ_{211}, δ_{010}, δ_{020} and δ_{121}), which are also shown in the bottom panel (b), represent different combinations of the temporal changes in A and B (i.e. the numbers of species present in both sites vs. either site). The seventh type (δ_{110}) indicates the number of species that were extirpated in one site but colonised the other site. The eighth and ninth types (δ_{111} and δ_{222}) indicate the number of species which showed no change in presence–absence statuses between two time points.

and unique species (A and B) between two time points. For the sake of compact notation, we write x, y or z for the number of sites in which a given species occurred at $t = 1$, $t = 2$ or at both $t = 1$ and 2 respectively (i.e. x is its frequency at $t = 1$, and y is its frequency at $t = 2$). We also write δ_{xyz} for the number of species corresponding to x, y and z. For example, δ_{100} is the number of species that were unique to one of the two sites at $t = 1$ and became absent at $t = 2$. We can then describe the number of species corresponding to each of the six types as δ_{100} (type 1), δ_{200} (2), δ_{211} (3), δ_{010} (4), δ_{020} (5) and δ_{121} (6) (Fig. 2b).

Types 1, 5 and 6 reduce the spatial community dissimilarity (D_p), leading to homogenisation, whereas types 2, 3 and 4 increase D_p, leading to heterogenisation (Fig. 2b). Note that types 1 and 4 can occur simultaneously for the same species, such that a unique species is extirpated from one site but colonises the other site during the same time interval. The number of species that meet such conditions is denoted as δ_{110} (Fig. 2a). These species do not alter D_p between two time points owing to their offsetting replacements of presence–absence status. However, such "hidden" species dynamics should be explicitly considered when quantifying the extent to which extirpations and colonisations cause communities to homogenise or heterogenise; we describe this in detail below. The numbers of unique and shared species that

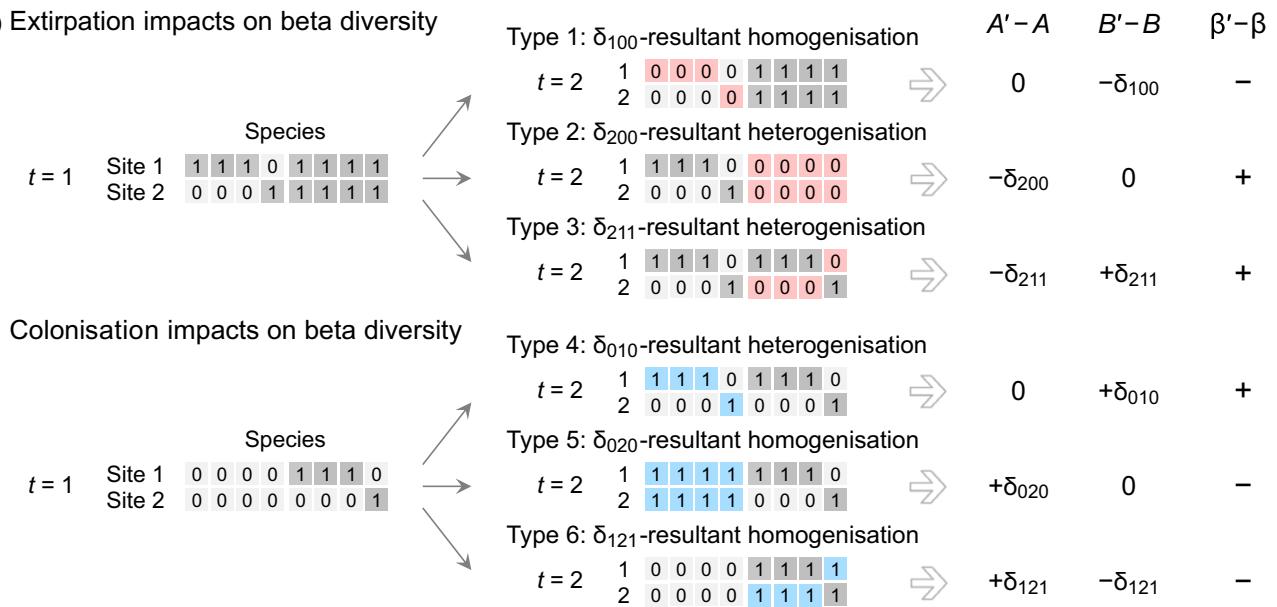remain unchanged are denoted as δ_{111} and δ_{222} respectively (Fig. 2a).

We can now additively partition the temporal changes in pairwise dissimilarity ($\Delta\beta_{\text{Total}}$) into six components: $\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$ and $\Delta\beta_6$. To distinguish the variables at $t = 1$ and $t = 2$, we add prime symbols to the latter cases (e.g. D_p'). The temporal changes in A and B can be described as $\Delta A = A' - A = \delta_{020} + \delta_{121} - \delta_{200} - \delta_{211}$ and $\Delta B = B' - B = \delta_{211} + \delta_{010} - \delta_{100} - \delta_{121}$. Their relative changes can be defined as $\lambda_A = \Delta A/A$ and $\lambda_B = \Delta B/B$, where A and B are both non-zero. We then get (see Appendix S1 for its derivation):

$$\Delta\beta_{\text{Total}} = D_p' - D_p = \underbrace{-\frac{G}{B}(\delta_{100} + \delta_{110})}_{\Delta\beta_1} + \underbrace{\frac{G}{A}\delta_{200}}_{\Delta\beta_2}$$
$$+ \underbrace{\left(\frac{G}{A} + \frac{G}{B}\right)\delta_{211}}_{\Delta\beta_3} + \underbrace{\frac{G}{B}(\delta_{010} + \delta_{110})}_{\Delta\beta_4} + \underbrace{\frac{-G}{A}\delta_{020}}_{\Delta\beta_5} + \underbrace{\left(-\frac{G}{A} - \frac{G}{B}\right)\delta_{121}}_{\Delta\beta_6},$$

(1)

where $G = \frac{D_p(1-D_p)}{(1-D_p)\lambda_A + D_p\lambda_B + 1}$ is a scaling factor. Mathematically, the numerator of G can be interpreted as the variance of probability D_p and the denominator as the ratio of the finite species pool size at $t = 2$ to that in $t = 1$ (see Appendix S1 for detail). The variables δ_{xyz} indicate the number of species that occurred in x-number of sites at $t = 1$, y-number of sites at $t = 2$ and z-number of sites at both $t = 1$ and 2 (Fig. 2a).

The six terms in eqn 1 reflect the effects of δ_{100}, δ_{200}, δ_{211}, δ_{010}, δ_{020} and δ_{121} (i.e. the number of species associated with each of the six types of extirpation and colonisation) and δ_{110} (i.e. the number of simultaneous occurrences of types 1 and 4) on $\Delta\beta_{\text{Total}}$ (Fig. 2). The quantities $-\frac{G}{B}\delta_{110}$ and $\frac{G}{B}\delta_{110}$ in terms $\Delta\beta_1$ and $\Delta\beta_4$ represent the "hidden" species dynamics, which obviously sum up to zero; that is, they cancel each other out. These two quantities thus allow us, without causing any effect on $\Delta\beta_{\text{Total}}$, to explicitly quantify the extent of homogenisation and heterogenisation driven by δ_{110}, in a manner comparable to $-\frac{G}{B}\delta_{100}$ and $\frac{G}{B}\delta_{010}$ respectively. We define the six terms as the extirpation components ($\Delta\beta_1$, $\Delta\beta_2$ and $\Delta\beta_3$) and the colonisation components ($\Delta\beta_4$, $\Delta\beta_5$ and $\Delta\beta_6$) of the temporal changes in pairwise dissimilarities.

Multiple-site variation

Additive partitioning of beta diversity can similarly be applied to multiple-site metrics such as Whittaker's beta (Whittaker 1960), defined as $\beta_W = \gamma/\bar{\alpha}$ (Fig. 2). Here, $\bar{\alpha}$ and γ are the mean species richness and the total number of species across sites respectively. Note that, in quantifying the compositional variation for cases with more than two sites, averaging the pairwise dissimilarities (e.g. β_J, β_S) across pairs of sites is a suboptimal approach given their lack of statistical independence (Baselga 2010, 2012). Whittaker's beta accounts for species co-occurrences in more than two sites and thus is an appropriate measure of multiple-site variation.

Although β_W is most often used in cases with more than two communities ($N \geq 3$), we start with the case of community

pairs ($N = 2$) for demonstration purposes. The temporal changes in $\bar{\alpha}$ and γ can be described as $\Delta\bar{\alpha} = \bar{\alpha}' - \bar{\alpha} = -\delta_{100}/2 -\delta_{200} - \delta_{211}/2 + \delta_{010}/2 + \delta_{020} + \delta_{121}/2$ and $\Delta\gamma = \gamma' - \gamma = -\delta_{100} - \delta_{200} + \delta_{010} + \delta_{020}$. Their relative amount of changes can be defined as $\lambda_{\bar{\alpha}} = \Delta\bar{\alpha}/\bar{\alpha}$ and $\lambda_\gamma = \Delta\gamma / \gamma$, where $\bar{\alpha}$ and γ are both non-zero. We then get (see Appendix S1 for its derivation):

$$\Delta\beta_{\text{Total}} = \frac{\gamma'}{\bar{\alpha}'} - \frac{\gamma}{\bar{\alpha}} = \underbrace{\left(\frac{H}{2\bar{\alpha}} - \frac{H}{\gamma}\right)(\delta_{100} + \delta_{110})}_{\Delta\beta_1} + \underbrace{\left(\frac{H}{\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{200}}_{\Delta\beta_2}$$
$$+ \underbrace{\frac{H}{2\bar{\alpha}}\delta_{211}}_{\Delta\beta_3} + \underbrace{\left(-\frac{H}{2\bar{\alpha}} + \frac{H}{\gamma}\right)(\delta_{010} + \delta_{110})}_{\Delta\beta_4} + \underbrace{\left(-\frac{H}{\bar{\alpha}} + \frac{H}{\gamma}\right)\delta_{020}}_{\Delta\beta_5} + \underbrace{\frac{-H}{2\bar{\alpha}}\delta_{121}}_{\Delta\beta_6},$$

(2)

where $H = \frac{\beta_W}{\lambda_{\bar{\alpha}} + 1}$ is a scaling factor, similar to G in eqn 1 (see Appendix S1 for its mathematical interpretations).

We define the six terms in eqn 2 as the extirpation and colonisation components of temporal changes in multiple-site variation (β_W) with two sites ($N = 2$). These definitions are in line with those based on the Jaccard and Sørensen indices (β_J and β_S) (eqn 1).

In eqns. 1 and 2, the extirpation component $\Delta\beta_1$ is always negative, whereas extirpation components $\Delta\beta_2$ and $\Delta\beta_3$ are both positive. We therefore refer to $\Delta\beta_1$ as extirpation-resultant homogenisation ($\Delta\beta_{E-}$) and the sum of $\Delta\beta_2$ and $\Delta\beta_3$ as extirpation-resultant heterogenisation ($\Delta\beta_{E+}$) (Fig. 1). For similar reasons, we refer to $\Delta\beta_4$ as colonisation-resultant heterogenisation ($\Delta\beta_{C+}$) and the sum of $\Delta\beta_5$ and $\Delta\beta_6$ as colonisation-resultant homogenisation ($\Delta\beta_{C-}$). Furthermore, depending on the ecological question at hand, one can sum the components together as $\Delta\beta_E = \Delta\beta_{E-} + \Delta\beta_{E+}$ and $\Delta\beta_C = \Delta\beta_{C-} + \Delta\beta_{C+}$ to determine the total extirpation- and colonisation-resultant changes respectively (Fig. 1).

Let us now expand the β_W-based additive partitioning to the case with three sites ($N = 3$), which can be described as (see Appendix S1 for its derivation):

$$\Delta\beta_{\text{Total}} = \frac{\gamma'}{\bar{\alpha}'} - \frac{\gamma}{\bar{\alpha}} = \underbrace{\left(\frac{H}{3\bar{\alpha}} - \frac{H}{\gamma}\right)(\delta_{100} + \delta_{110} + \delta_{120})}_{\Delta\beta_{E-}} + \underbrace{\left(\frac{2H}{3\bar{\alpha}} - \frac{H}{\gamma}\right)(\delta_{200} + \delta_{210})}_{\Delta\beta_{E-} \text{ or } \Delta\beta_{E+}}$$
$$+ \underbrace{\left(\frac{H}{\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{300} + \frac{H}{3\bar{\alpha}}(\delta_{211} + \delta_{221}) + \frac{2H}{3\bar{\alpha}}\delta_{311} + \frac{H}{3\bar{\alpha}}\delta_{322}}_{\Delta\beta_{E+}}$$
$$+ \underbrace{\left(-\frac{H}{3\bar{\alpha}} + \frac{H}{\gamma}\right)(\delta_{010} + \delta_{110} + \delta_{210})}_{\Delta\beta_{C+}} + \underbrace{\left(-\frac{2H}{3\bar{\alpha}} + \frac{H}{\gamma}\right)(\delta_{020} + \delta_{120})}_{\Delta\beta_{C-} \text{ or } \Delta\beta_{C+}}$$
$$+ \underbrace{\left(-\frac{H}{\bar{\alpha}} + \frac{H}{\gamma}\right)\delta_{030} - \frac{H}{3\bar{\alpha}}(\delta_{121} + \delta_{221}) - \frac{2H}{3\bar{\alpha}}\delta_{131} - \frac{H}{3\bar{\alpha}}\delta_{232}}_{\Delta\beta_{C-}}$$

(3)

Here, the terms can no longer be categorised *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 $\bar{\alpha}$ and γ. Notwithstanding this data dependence, however, the terms can be summed by groups such that they represent extirpation- and colonisation-resultant homogenisation and heterogenisation ($\Delta\beta_{E-}$, $\Delta\beta_{E+}$, $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$). Note that x, y and z can now have a maximum

value of 3 because of the increase to three sites. The symbols δ_{110}, δ_{221}, δ_{120} and δ_{210} in eqn 3 denote simultaneous extirpations and colonisations (i.e. the hidden species dynamics; see Appendix S1 for details).

To describe why some terms in eqn 3 can be either negative or positive, let us take the terms $\left(\frac{H}{3\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{100}$, $\left(\frac{2H}{3\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{200}$ and $\left(\frac{H}{\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{300}$ as examples. The symbols δ_{100}, δ_{200} and δ_{300} indicate extirpations of species that existed in one, two and three of the three sites respectively. The mean species richness $\bar{\alpha}$ is minimised when each species occurs in one site ($\frac{1}{3}\gamma$) and is maximised when all species occur in all three sites (γ). Thus, $\left(\frac{H}{3\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{100}$ is always negative and $\left(\frac{H}{\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{300}$ is positive. These mathematical results agree well with our intuition that extirpations of rare species (δ_{100}) result in biotic homogenisation, whereas extirpations of widespread species (δ_{300}) lead to heterogenisation (Socolar *et al.* 2016; Tatsumi *et al.* 2020). On the other hand, $\left(\frac{2H}{3\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{200}$ can change its sign depending on the balance between $\bar{\alpha}$ and γ. This also makes sense, given that whether the extirpations of common species (δ_{200}) drive homogenisation or heterogenisation is contingent upon the frequencies of all species across the sites. In other words, regardless of the frequency of a given species *per se*, eqn 3 allows us to flexibly quantify the effects of its dynamics on $\Delta\beta_{Total}$, with consideration given to the compositional structure over the entire community dataset.

Following eqns 2 and 3, the additive partitioning of temporal changes in β_W for N sites can be generalised as (see Appendix S1 for its derivation):

$$\Delta\beta_{Total} = \frac{\gamma'}{\bar{\alpha}'} - \frac{\gamma}{\bar{\alpha}} = \underbrace{\sum_{x>z=0}\left(\frac{xH}{N\bar{\alpha}} - \frac{H}{\gamma}\right)\delta_{xyz}}_{\Delta\beta_{E-} \text{ or } \Delta\beta_{E+}} + \underbrace{\sum_{x>z>0}\frac{(x-z)H}{N\bar{\alpha}}\delta_{xyz}}_{\Delta\beta_{E+}} + \underbrace{\sum_{y>z=0}\left(-\frac{yH}{N\bar{\alpha}} + \frac{H}{\gamma}\right)\delta_{xyz}}_{\Delta\beta_{C-} \text{ or } \Delta\beta_{C+}} + \underbrace{\sum_{y>z>0}\frac{(z-y)H}{N\bar{\alpha}}\delta_{xyz}}_{\Delta\beta_{C-}}$$

$$(4)$$

The sums of the negative and positive terms represented by $\Delta\beta_{E-}$ and $\Delta\beta_{E+}$ indicate extirpation-resultant homogenisation and heterogenisation respectively. Similarly, those represented by $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$ show colonisation-resultant homogenisation and heterogenisation respectively. Importantly, $\Delta\beta_{E-}$ and $\Delta\beta_{C+}$ reflect the dynamics of species that are less common (frequent) than average, whereas $\Delta\beta_{E+}$ and $\Delta\beta_{C-}$ indicate those that are more common than average. Here, the "commonness" of a species is assessed quantitatively from the compositional structure across all sites, as described above.

Species-level impacts on beta diversity

We can further use eqns 1, 2, 3 and 4 to quantify the effects of extirpations and colonisations of any individual species on beta diversity (Fig. 1). For example, consider an extirpation event for a species that existed in one out of N sites. This event will increase δ_{100} by 1. According to the coefficients (or multiplicands) of δ_{100} in the equations, increasing δ_{100} by 1 will translate into adding $-\frac{G}{B}$ (eqn 1) or $\left(\frac{H}{N\bar{\alpha}} - \frac{H}{\gamma}\right)$ (eqns 2, 3

and 4) to $\Delta\beta_{Total}$. These added values thus reflect the consequence of the focal species' extirpation on beta diversity. In this way, $\Delta\beta_{Total}$ can be additively partitioned into components that reflect species-level extirpations and colonisations, namely $\Delta\beta_{Sp}$ (Fig. 1).

Note that it is possible for a species to be extirpated in one or more sites but colonise one or more other sites within the same time interval. In such cases, the species will generate two components in terms of its impact on beta diversity. Illustrating this in Fig. 1, the components will appear separately in the left (red) and right (blue) columns in the bottom row. Also note that any given species can neither be extirpated nor colonise a site and will thus drive no change in beta diversity. As such, the number of species-level components ($\Delta\beta_{Sp}$) would not necessarily equal the number of species observed.

Sensitivity analyses

The size of each extirpation and colonisation component ($\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$, $\Delta\beta_6$, $\Delta\beta_{E-}$, $\Delta\beta_{E+}$, $\Delta\beta_{C-}$ and $\Delta\beta_{C+}$) should reflect species dynamics (δ_{xyz}) in a way that is consistent with its definition. For example, extirpation-resultant homogenisation $\Delta\beta_{E-}$ ($\Delta\beta_1$) must be non-positive and decrease with the extirpation of unique species (δ_1) (Fig. 2b). Whether such conditions are met can be verified by means of sensitivity analyses. Here, we vary one of the nine variables δ_{100}, δ_{200}, δ_{211}, δ_{010}, δ_{020}, δ_{121}, δ_{110}, δ_{111} and δ_{222} from 0 to 100 while fixing the others at 10. We then calculate the extirpation and colonisation components based on the Jaccard and Sørensen indices (β_J and β_S; eqn 1) and on Whittaker's beta (β_W; eqn 2). Below, we show the outcomes based on β_S in Fig. 3; those based on β_J and β_W are provided in Appendix S2, as they were comparable to the results with β_S.

The sensitivity analyses confirmed that the component $\Delta\beta_{E-}$ ($\Delta\beta_1$) decreases with the extirpations of unique species (δ_{100}), whereas the component $\Delta\beta_{E+}$ ($\Delta\beta_2$ and $\Delta\beta_3$) increases with the extirpations of shared species (δ_{200} and δ_{211}) (Fig. 3a, b, c). Similarly, for colonisation, $\Delta\beta_{C+}$ ($\Delta\beta_4$) increases with unique species (δ_{010}), whereas $\Delta\beta_{C-}$ ($\Delta\beta_5$ and $\Delta\beta_6$) decreases with shared species (δ_{020} and δ_{121}) (Fig. 3d, e, f). 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 δ_{100}, δ_{200}, δ_{211}, δ_{010}, δ_{020} and δ_{121} (Fig. 3a, b, c, d, e, f). This finding agrees well with the fact that $\Delta\beta_3$ and $\Delta\beta_6$ reflect numerical changes in both unique and shared species (see types 3 and 6 in Fig. 2b), whereas the other $\Delta\beta$ components are responsible for either unique or shared species (types 1, 2, 4 and 5). Furthermore, consistent with its definition, the hidden species dynamics (δ_{110}) simultaneously decrease $\Delta\beta_1$ and increase $\Delta\beta_4$ without affecting $\Delta\beta_{Total}$ (Fig. 3g). Species that show no change in their presence–absence statuses (δ_{111} and δ_{222}) cause no impact on $\Delta\beta_{Total}$ but reduce the relative importance of other species (Fig. 3h, i).

APPLICATIONS

Using two empirical datasets, we highlight how the partitioning method developed here can provide new insights into
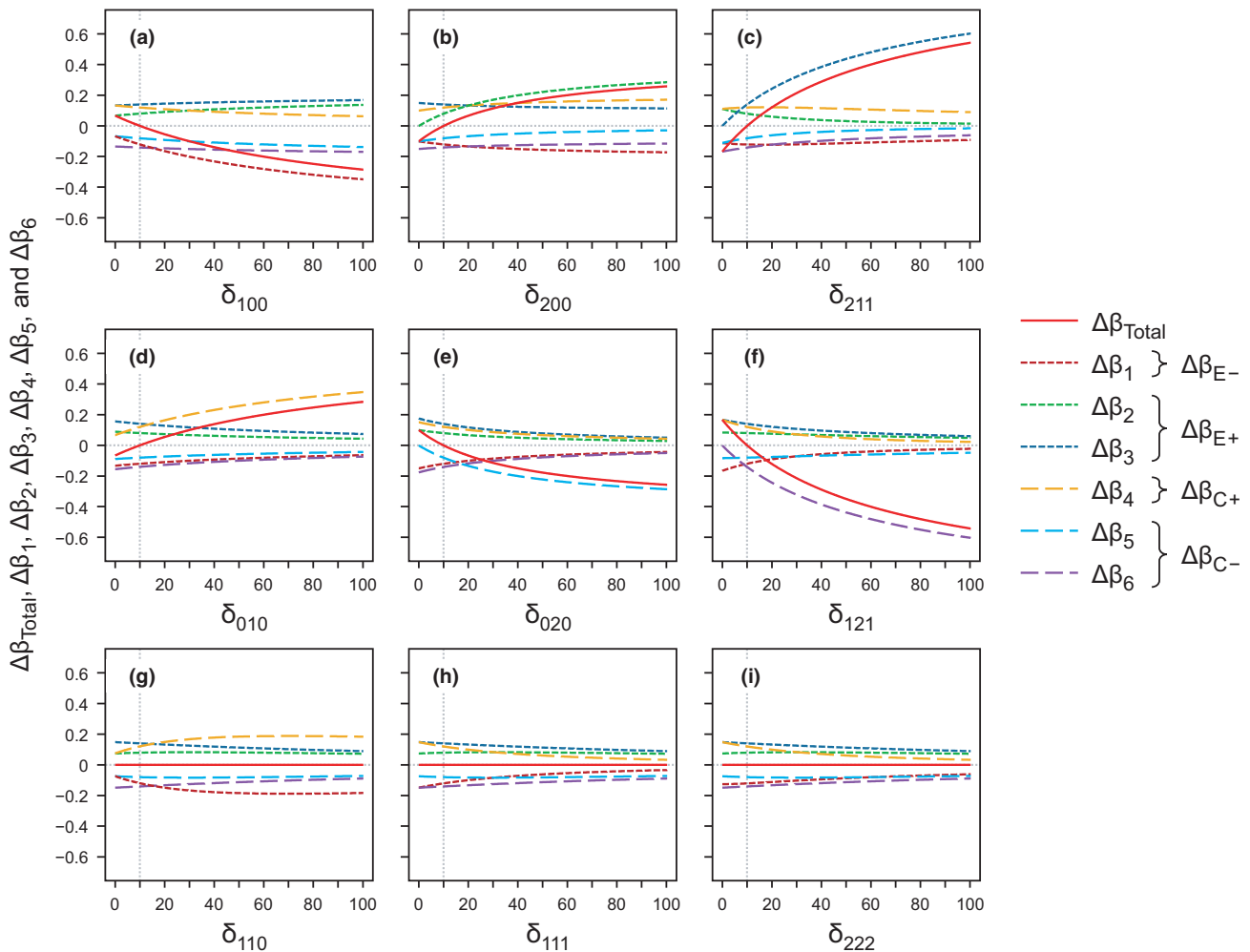
Figure 3 Sensitivity analyses of the response of temporal changes in beta diversity ($\Delta\beta_{\text{Total}}$) and its components ($\Delta\beta_1$, $\Delta\beta_2$, $\Delta\beta_3$, $\Delta\beta_4$, $\Delta\beta_5$ and $\Delta\beta_6$) to varying numbers of unique and shared species (δ_{xyz}; see Fig. 2 for their visual representation). Examples are shown using the Sørensen beta diversity index; comparable examples for the Jaccard and Whittaker's beta diversity indices are shown in Appendix S2. In each panel, the values of δ_{xyz} were fixed at 10 (indicated by vertical lines) except for the index shown on the *x*-axis, whose value was varied from 0 to 100.

spatiotemporal community assembly. An R script 'ecopart.R' (Extinction and COlonisation PARTitioning) which executes the calculation in R (R Core Team 2020) is provided in Appendix S3.

Application 1: Tree communities in mature forests

We first analysed tree-census data collected in permanent forest plots across Japan (Ishihara *et al.* 2011). From the original dataset publicly available (http://www.biodic.go.jp/moni1000/findings/data/index_file.html), we used a subset of 34 mature-forest plots with no signs of a recent disturbance event (see Appendix S4 for detailed selection criteria). The plots are typically 100 m × 100 m in size and are composed of 10-m × 10-m subplots (see Appendix S4 for the exact size of each plot). Trees with stem diameter at breast height > 4.8 cm have been repeatedly recorded as species presence–absence data in each plot. We defined beta diversity in each plot as the ratio of the total species richness to the mean richness among the subplots ($\beta_W = \gamma/\bar{\alpha}$). The temporal changes in beta diversity ($\Delta\beta_{\text{Total}}$)

and their components ($\Delta\beta_E$ and $\Delta\beta_C$) were calculated from two time points spanning 10 years between 2004–2008 and 2014–2018. With this dataset, we tested whether extirpations and colonisations occurred substantial enough to alter the spatial variation in tree communities by applying one-sample *t*-tests to $\Delta\beta_{\text{Total}}$, $\Delta\beta_E$ and $\Delta\beta_C$.

The partitioning method revealed significant community dynamics that were otherwise undetectable. First, tree communities in these mature-forest plots showed no net change in beta diversity through time ($\Delta\beta_{\text{Total}}$) (Fig. 4; Appendix 5). From this result, we might conclude that there was no directional species turnover that forced changes in the extent of spatial community variation. However, when $\Delta\beta_{\text{Total}}$ was partitioned into extirpation and colonisation components ($\Delta\beta_E$ and $\Delta\beta_C$), we found significant trends in both components (Fig. 4). Specifically, the mean $\Delta\beta_E$ was significantly greater than 0 ($P < 0.001$), indicating that multiple species, typically widespread species, were extirpated across the subplots within each plot, thus increasing spatial variation. On the other hand, the mean $\Delta\beta_C$ was significantly lower than 0 ($P < 0.01$),
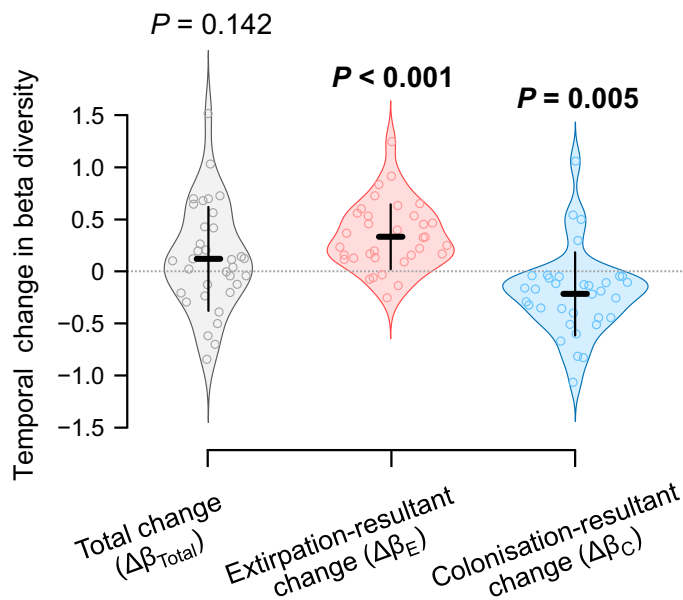
Figure 4 Temporal changes in beta diversity and its extirpation and colonisation components between two time points spanning 10 years in 34 permanent tree-census plots across Japan. Beta diversity in each plot, typically 100 m × 100 m in size, was calculated as the ratio of the total species richness to the mean species richness across 10-m × 10-m subplots ($\beta = \gamma/\bar{\alpha}$). Horizontal and vertical bars indicate sample means ± SD. Shaded areas show the probability densities of the samples. P-values indicate the significance of the difference between the sample mean and 0 (one-sample t-test).

suggesting that the among-subplot colonisations overwhelmed the colonisations of new species from outside each plot, thereby increasing similarity among the subplots. Consequently, when the two processes were combined ($\Delta\beta_{Total}$), they masked each other out (Fig. 4). The partitioning of the extirpation and colonisation components uncovered significant yet cryptic community dynamics in mature forests that have long been free of disturbance.

Alpha and gamma diversity of the tree communities did not change between the 10-year interval (Appendix S5). The absolute sizes of extirpation and colonisation components showed increasing trends in response to the initial beta diversity at $t = 1$ (Appendix S6).

Application 2: Coral communities subject to environmental perturbations

As a second example of our partitioning method, we analysed a dataset of coral communities on a reef flat south of Tikus Island, Indonesia (Brown & Suharsono 1990; data found in Anderson *et al.* 2011). The dataset consisted of coral communities recorded along $N = 10$ permanent transects on six occasions between 1981 and 1988, before and after an El Niño event in 1982–1983. We defined beta diversity in a given survey year as the ratio of the total species richness to the mean richness among the transects. The temporal changes in beta diversity and their components were calculated between pairs of survey years. We also determined the species-level impacts of extirpations and colonisations on beta diversity. In contrast to the
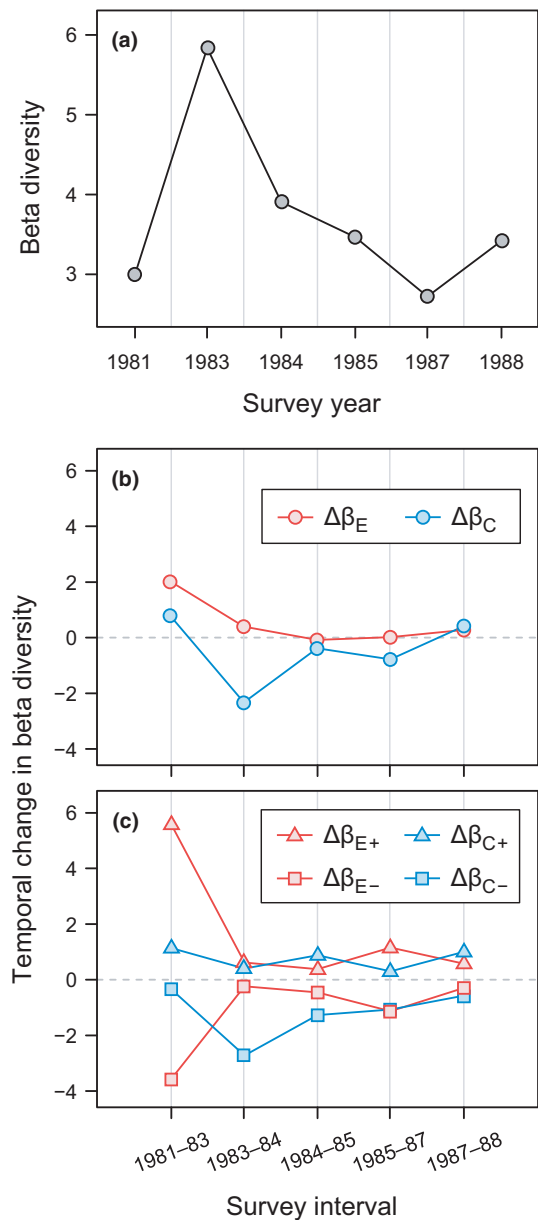

Figure 5 Beta diversity of coral communities on a reef flat in Indonesia. (a) Beta diversity in six survey years between 1981 and 1988, before and after an El Niño event in 1982–1983. (b) Extirpation- and colonisation-resultant changes in beta diversity between pairs of survey years. $\Delta\beta_E$ and $\Delta\beta_C$, extirpation- and colonisation-resultant changes; β_{E-} and $\Delta\beta_{E+}$, extirpation-resultant homogenisation and heterogenisation and $\Delta\beta_{C+}$, and $\Delta\beta_{C-}$, colonisation-resultant homogenisation and heterogenisation

non-disturbed forests, the coral communities allowed for quantification of extirpation and colonisation dynamics induced by a demonstrable environmental perturbation (i.e. El Niño).

The beta diversity of coral communities increased after the 1982–1983 El Niño event and then gradually returned to the initial level (Fig. 5a). The alpha and gamma diversity decreased after the event (Appendix S5). The partitioning method revealed that both extirpations and colonisations played important roles in beta diversity changes between 1981 and 1983 (Fig. 5b). The El Niño event caused extirpations of

Table 1 Species-level impacts on beta diversity in coral communities on a reef flat in Indonesia. For each survey interval, the top three species in terms of the absolute values of total $\Delta\beta_{Sp}$ (right columns) are shown

| Survey interval | Species | Number of occurrences* (N = 10) | | | Species-level impact on beta diversity ($\Delta\beta_{Sp}$) | | |
		$t = 1$	$t = 2$	$t = 1$ and 2	Extirpation	Colonisation	Total
1981–1983	*Favites abdita*	10	0	0	0.556	0	0.556
	Acropora aspera	9	0	0	0.472	0	0.472
	Pocillopora damicornis and *Acropora diversa*	8	0	0	0.389	0	0.389
1983–1984	*Montipora digitata*	1	9	1	0	−0.631	−0.631
	Montipora monasteriata	0	7	0	0	−0.417	−0.417
	Montipora foliosa	1	6	1	0	−0.394	−0.394
1984–1985	*Porites nigrescens*	1	10	1	0	−0.371	−0.371
	Montipora tuberculosa	2	6	2	0	−0.165	−0.165
	Porites cylindrica	4	8	4	0	−0.165	−0.165
1985–1987	*Porites nigrescens*	10	2	2	0.421	0	0.421
	Acropora hyacinthus	1	5	1	0	−0.211	−0.211
	Porites cylindrica	8	4	4	0.211	0	0.211
1987–1988	*Porites nigrescens*	2	9	2	0	−0.262	−0.262
	Montipora digitata	8	5	5	0.112	0	0.112
	Acropora humilis, Acropora diversa, Acropora divaricata, and *Acropora millepora*	0	1	0	0	0.100	0.100
1981–1988	*Favites abdita*	10	1	1	0.370	0	0.370
	Acropora diversa	8	1	0	0.192	0.096	0.288
	Pocillopora damicornis	8	2	0	0.192	0.055	0.247

*The number of transects in which a given species occurred at $t = 1$ (the begininng of survey interval), $t = 2$ (the end of survey interval) and at both $t = 1$ and 2.

multiple species across sites, as indicated by high $\Delta\beta_{E+}$ and low $\Delta\beta_{E-}$ (Fig. 5c). In particular, widespread species were excluded more substantially than rare species ($|\Delta\beta_{E+}| > |\Delta\beta_{E-}|$), leading to an overall increase in beta diversity (Fig. 5a, b). The species-level analyses revealed that this increase was attributable to extirpations of initially widespread species such as *Favites abdita* and *Acropora aspera* (Table 1). The El Niño event also induced spatially sporadic colonisation of new species, as was indicated by relatively high $\Delta\beta_{C+}$ and positive $\Delta\beta_C$ between 1981 and 1983 (Fig. 5b, c).

The reduction in beta diversity during the subsequent years was driven mostly by species colonisations, whereas extirpations played minor roles ($\Delta\beta_E \approx 0$) (Fig. 5b). The post-El Niño community reassembly was characterised by spatially uniform colonisation of species that were initially rare (e.g. *Montipora* spp.; Table 1), as indicated by low $\Delta\beta_{C-}$ and negative $\Delta\beta_C$ (Fig. 5b, c). After 1987, there were sporadic colonisations of new species such as *Acropora* spp. (Table 1), which resulted in a slight increase in beta diversity (Fig. 5a, b). Overall, the partitioning approach enabled detailed quantification of how different species contributed to community disassembly and reassembly induced by the El Niño event. It also revealed that the relative importance of extirpations and colonisations *per se* changed temporally after the environmental perturbation.

DISCUSSION

Ecologists have long recognised that beta diversity can either decrease or increase in response to extirpations and colonisations (Vitousek 1997; McKinney & Lockwood 1999; Olden &

Rooney 2006; Socolar *et al.* 2016; Tatsumi *et al.* 2020). However, analytical challenges have hampered our ability to disentangle the impact of these dynamic processes on temporal changes in beta diversity (Baeten *et al.* 2014; Tatsumi *et al.* 2020). Here, we derived equations that partition the temporal changes in pairwise (Jaccard and Sørensen) and multiple-site dissimilarity measures (Whittaker's beta) into distinct terms reflecting extirpations and colonisations (Fig. 1). By applying this method to empirical datasets, we found non-random spatiotemporal dynamics in tree and coral communities (Figs 4 and 5). The method also enabled detailed assessments of species-level impacts on $\Delta\beta_{Total}$ (Table 1). Our method is applicable to any taxonomic grouping at any spatial and temporal scale. With the growing availability of spatially and temporally replicated ecological data (e.g. BioTIME; Dornelas *et al.* 2018), the partitioning method can help discern the dynamic processes behind changes in biodiversity.

The equations derived in this study provide theoretical underpinnings for the use of beta diversity in biological conservation (Olden 2006; Myers & LaManna 2016; Socolar *et al.* 2016). Importantly, increasing the frequency (i.e. the number of sites in which a species is present) of a rare species that already exists in a region does not increase, but rather decreases, beta diversity, as is clarified by the negative fourth term of eqn 4. Theoretically, the only way to increase beta diversity via colonisation is through sporadic colonisation of new species that were regionally absent (Socolar *et al.* 2016; Tatsumi *et al.* 2020). This means that the sign (positive or negative) of colonisation-resultant changes in beta diversity depends on whether the species have been previously detected

in the region. Therefore, the spatial scale of the region and the intensity of surveys (e.g. detection rates) require careful consideration in conservation planning.

The fact that the second term of eqn 4 is positive indicates that the extirpations of any species, no matter how rare or widespread, increase beta diversity as long as the species is not excluded from all the communities being studied (i.e. as long as its regional frequency remains greater than 0). Extirpations will decrease beta diversity only if the frequency of a given rare species becomes 0 (Socolar *et al.* 2016; Tatsumi *et al.* 2020). As such, even when the frequency of a species gradually decreases to 0 at a steady pace, the associated changes in beta diversity will show temporally nonlinear trends. Such theoretical perspectives based on our equations should help us determine the spatiotemporal scales and management strategies that best suit regional conservation goals.

Different classes of ecological mechanisms (e.g. drift, selection, dispersal and speciation; Velland 2010) can underlie the extirpation and colonisation components of $\Delta\beta_{Total}$ (Fig. 1). For example, extirpation-resultant homogenisation ($\Delta\beta_{E-}$) can reflect stochastic extinctions of regionally rare species. Specifically, declines in community size (e.g. caused by disturbance) can increase the importance of ecological drift, through which species with lower frequencies are more likely to go extinct (Caswell 1976; Hubbell 2001; Velland 2010), and thereby reducing beta diversity. Alternatively, extirpation may increase community variation ($\Delta\beta_{E+}$) if negative density-dependent selection (e.g. caused by intraspecific competition or frequency-dependent predation; Chesson 2000) reduces the frequencies of widespread species more strongly than those of rare species. Colonisation-resultant homogenisation ($\Delta\beta_{C-}$) can occur when new species with high dispersal ability spread across the region (i.e. internal dispersal within a given metacommunity; Fukami 2015; Tatsumi *et al.* 2020) or when the initial pool of species is constrained by dispersal filters (i.e. limited external dispersal from outside the metacommuniy; Velland *et al.* 2007; Mueller *et al.* 2016). Colonisation-resultant heterogenisation ($\Delta\beta_{C+}$) can, over long time scales, result from speciation, whereby new species are added to local communities (Condit 2002). As such, our method has strong links with processes inherent to coexistence and metacommunity theory (i.e. density-dependent interactions, abiotic filtering and dispersal limitation; Chesson 2000; Leibold & Chase 2017; Thompson *et al.* 2020) and thus could be utilised for their empirical testing.

There is still room for further development in our partitioning method. First, our empirical analyses showed increasing trends in the absolute sizes of extirpation and colonisation components with the initial beta diversity (β_W at $t = 1$) (Appendix S6). Mathematically, this tendency is likely inevitable, considering that the components contain β_W in their numerators (see H in eqn 2). In fact, this non-independence itself (i.e. the phenomenon that greater spatial variation bears larger temporal changes) could reflect metacommunity processes (e.g. drift) and thus be an important topic for future work. Developing a null model that increases the statistical independency among the measures (Gotelli *et al.* 2017; Legendre 2019) would also be a potential extension of our method. Another promising way forward is to account for species

abundances and to distinguish the spatial replacement and nestedness components of beta diversity (Baselga 2010, 2012). The latter components, however, can show complex nonlinear relationships with extirpations and colonisations (Lu et al. 2019). The feasibility of their temporal partitioning is thus unclear and something that should be addressed in the future.

It should be noted that our partitioning method on its own cannot ascertain the underlying causes of spatially non-random extirpations and colonisations. However, in combination with controlled experiments, demonstrable environmental gradients, or stochastic events such as disturbance (Cadotte & Tucker 2017), the partitioning of extirpation and colonisation components can help us draw more direct links between changes in beta diversity and the likely ecological mechanisms. Moreover, associations between the estimated impacts of individual species ($\Delta\beta_{Sp}$; Fig. 1) and their functional traits (e.g. propagule sizes and their relationship to dispersal ability) could corroborate such links. Moving forward, open questions include determining: (1) the spatiotemporal scales that are most or least relevant to extirpation- and colonisation-resultant changes in beta diversity, (2) functional traits associated with species' vulnerability or capability regarding such changes and (3) the anthropogenic factors that are causing the greatest impacts on spatially non-random species losses and gains. We believe that explicit analyses of the extirpation--colonisation processes underlying beta diversity should bring deeper insights into the (re)organisation of biodiversity across space and time.

AUTHORSHIP

ST conceived the study, RI and ST developed the methodology, ST analysed the data and wrote the first draft of the manuscript with inputs from MWC and RI, and all authors contributed to revision and editing.

DATA ACCESSIBILITY STATEMENT:

The tree census dataset is publicly available at the website of the Biodiversity Center of Japan (the Monitoring Sites 1000 Project; http://www.biodic.go.jp/moni1000/findings/data/index_file.html). The coral community dataset is found in Anderson et al. (2011).

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13720.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.