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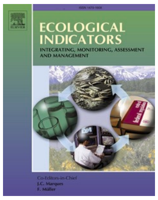

Original Articles

New measures for quantifying directional changes in presence-absence community data

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ABSTRACT

Variation in community composition and species turnover are different types of beta diversity, expressing non-directional and directional changes, respectively. While directional changes (e.g. turnover) along geographic gradients can be studied in any direction depending on the hypothesis of interest to researchers, temporal changes can only be meaningfully studied from past to present. Although a wide variety of methods exist for partitioning variation and related community-level phenomena such as similarity, richness difference and nestedness, approaches evaluating species turnover along geographic or temporal gradients, based on an analogous conceptual framework, are rare. We therefore look into the possibilities for examining different aspects of directional changes along a gradient when presence-absence community data are available. Measures of community overlap, as well as species loss and gain from one sampling unit to another along a gradient are combined to define a variety of turnover and nestedness concepts and to derive functions for their quantification. Each concept represents an ecological phenomenon to be indicated (indicandum), whereas measures (indicators) quantify relevant properties of these concepts. The measures use the raw number of species as well as relativized forms in accordance with the well-known Jaccard and Sørensen indices. The main innovation is the development of new measures of directional community change. We demonstrate differences between traditional non-directional and the new directional measures and use several examples to show that actual communities display directional responses to a particular ecological gradient. The new measures therefore reveal an uncovered aspect of community ecology.

1. Introduction

The original concept of beta diversity (Whittaker, 1960) has long been used in a wide variety of theoretical and empirical frameworks in community ecology and macroecology for quantifying the extent of change in species composition along gradients or for measuring compositional heterogeneity among sampling units (Shmida and Wilson, 1985; Vellend, 2001). Accordingly, Anderson et al. (2011) have distinguished between two types of beta diversity: turnover along gradients and non-directional variation. Turnover reflects directional changes in a community from one sampling unit to another along a spatial, temporal, or environmental gradient, whereas community variation expresses non-directional changes in the biological composition of sampling units taken within a given spatial or temporal extent. According to these definitions, methods for studying variation in community composition along a continuous gradient (e.g. Tatsumi et al., 2021) belong to the *variation* type of beta diversity analysis (see Fig. 4 of Anderson et al., 2011 for details about the available methods) and are thus out of the scope of the present study. Note also that whereas turnover along geographic gradients can be studied in any direction, depending on the hypothesis the researcher is interested in, temporal directional changes in communities can only be meaningfully studied from the past to the present, following the asymmetry in the degradation of energy stated in the second law of thermodynamics.

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Precise definition of turnover should refer to a *directional change in a community* ("How many new species are encountered along a gradient and how many that were initially present are now lost?" Anderson et al., 2011). When we move, for instance, from 600 m above sea level (a.s.l.) to 1100 m a.s.l., we can observe *gain* and *loss* of species, or else no change in species composition (the same species are present at both sites, see Fig. 1). If we detect a decrease in species richness (which implies *species loss*), then we are concerned with a *negative directional change* in richness in the community. However, the *same difference becomes positive* if we go down the mountainside. This means that *change in a community can be characterized by considering direction*. Directionality is provided either by time, or as the result of a directional physical process that acted through time in the past and whose results are being studied. Directionality receives less attention when studying temporal community changes because time is unidirectional and community changes are routinely examined over time from earlier to later dates (see Dornelas et al., 2013; Legendre, 2019; Magurran et al., 2019). However, traditional uses of dissimilarity coefficients to study temporal changes disregard the asymmetry of time processes, which is obvious; hence, the dissimilarity coefficients are not called upon to assess changes through time with special indication of directionality.

Baselga (2010) pioneered the idea that beta diversity can be partitioned into replacement and nestedness-resultant components. The method; called BAS partitioning (Legendre, 2014), has been considered as a major novelty in biodiversity research because the components may reflect the existence of different mechanisms underlying beta diversity. Thus, the method can be used efficiently for revealing geographic and ecological factors that influence community composition and for understanding conservation issues. Thanks to its originality and soundness, Baselga's procedure triggered critical comments, an intensive dispute, and the development of alternative approaches (Baselga, 2010; Baselga, 2012; Almeida-Neto et al., 2012; Carvalho et al., 2013; Legendre, 2014; Podani and Schmera, 2016). One of the newer approaches, called the SDR (**S**imilarity, richness **D**ifference and **R**eplacement) simplex method (Podani and Schmera, 2011), is more exhaustive by exploring the inherent structure of community pattern (see also Podani et al., 2018). It means that the SDR simplex method deals not only with beta diversity and its components, but allows the evaluation of similarity, nestedness, agreement in species richness and related community-level phenomena, within a single, unified methodological framework.

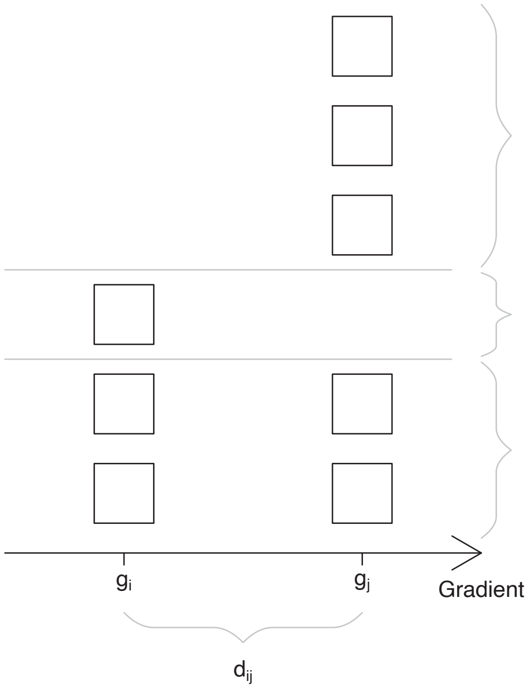

Fig. 1. A pattern of pairs of sampling units (pairwise pattern) shows community changes form one position (g_i) to another (g_j) along a directional gradient. The pairwise pattern can be divided into Overlap, Loss, and Gain PPCs. Squares represent species presences.

Although the BAS and SDR methods include variation-type beta diversity components, these methodologies are frequently used for characterizing community change along gradients (Suppl. Document 1). In most cases, however, the gradient involved and the factor explaining changes in beta diversity were not the same. For example, Zedková et al. (2015) evaluated beta diversity and its components for mayfly assemblages between two time periods (1955–1960 and 2006–2011) in relation to a stream size gradient (in brooks, small and large rivers). In this example, the ecological gradient studied was stream size, while beta diversity reflected temporal differences between the study periods. With this example, we by no means state that the study of Zedková et al. (2015) is scientifically irrelevant but emphasize that it cannot reveal the *directed* effect of the ecological gradient (stream size) on beta diversity (temporal). A noted exception is presented by Marini et al. (2013); who studied how relative richness difference and relative species replacement components were related to the elevational difference of site pairs in plant communities along an altitudinal gradient (see their Fig. 3). Such analyses, however, clearly restrict possible inferences, because the available approaches include exclusively variation-type (*non-directional)* measures, which are inadequate for expressing *directional changes*.

Surprisingly, directional measures received only limited attention (Koleff et al., 2003). To assess directional community changes, we suggest new directional indices. The new idea is based on the decomposition of temporal beta diversity into loss and gain components (as in Legendre, 2019; Magurran et al., 2019; Wu et al., 2020), on *P*airwise *P*attern *C*omponents (PPCs, Schmera et al., 2020) and on the SDR simplex method (Podani and Schmera, 2011). We show that directional changes in a community *per se* can be characterized further in terms of its individual components – specifically, the degree of overlap, gains and losses in species – to enrich our understanding of community changes. We suggest that directional changes in a community from one sampling unit to another along a gradient (i.e. turnover, Anderson et al., 2011) can be further qualified as gaining turnover (turnover dominated by the gain of species), neutral turnover (balanced gain and loss of species) and losing turnover (turnover dominated by loss).

Similarly, we show that although nestedness is defined as "the ordered loss of species along environmental or ecological gradients" (Ulrich and Almeida-Neto, 2012), the concept is rarely assessed along ecological gradients (see review in Podani and Schmera, 2012); but see also Kunin (1995) and Almeida-Neto et al. (2008). We argue that species loss and gain must be distinguished and suggest that nestedness along a gradient be further interpreted as gaining nestedness (nestedness with species gain), neutral nestedness (nestedness without richness modification) and losing nestedness (nestedness with species loss). Finally, we demonstrate the performance of these measures using artificial as well as real datasets coming from studies of fossil and extant animal assemblages.

2. The new measures

2.1. Conceptual background

To characterize directional change in community pattern from one sampling unit observed at a particular gradient position (g_i) to another sampling unit taken elsewhere along the directional gradient (g_j), and following Legendre (2019); we suggest three *PPCs*: *Overlap*, *Gain* and *Loss* (*a, c* and *b* in Legendre, 2019). Of these, Overlap is the similarity component; it is also part of the indices used in non-directional analysis (Schmera et al., 2020); it refers to species that are present in both sampling units. The Gain and Loss *PPCs* are novel components even if gain and loss are well-known terms in community ecology, especially in

Table 1

Concepts and the corresponding raw measures for directional analysis of community change between two sampling units quantified by the number of species.

Concept	Note	Measure	Reference
overlap	number of species present in both sites	a	(Podani and Schmera, 2011)
species gain	number of species present only in the second site along the directed gradient	c	(Legendre, 2019)
species loss	number of species present only in the first site along the directed gradient	b	(Legendre, 2019)
gaining turnover (=turnover dominated by gain)	richness change (b-c) is negative	if $c > b$, then $b + c$, else 2 min(b,c)	this paper
neutral turnover (=turnover with balanced gain and loss)	there is no richness modification	2 min(b,c)	this paper
losing turnover (=turnover dominated by loss)	richness change (b-c) is positive	if $b > c$, then $b + c$, else 2 min(b,c)	this paper
gaining nestedness (=nestedness with species gain)	some species are present in both sites ($a > 0$) and richness change (b-c) is negative	if $a > 0$ and b-$c < 0$, then a+|b-c| if $a > 0$ and b-$c \geq 0$, then a if $a = 0$, then 0	this paper
neutral nestedness (=nestedness without richness modification)	some species are present in both sites ($a > 0$) and there is no richness modification b-c = 0	if $a > 0$, then a if $a = 0$, then 0	this paper
losing nestedness (=nestedness with species loss)	some species are present in both sites ($a > 0$) and richness change (b-c) is positive	if $a > 0$ and b-$c > 0$, then a+|b-c| if $a > 0$ and b-$c \leq 0$, then a if $a = 0$, then 0	this paper
gaining strict nestedness (=strict nestedness with species gain)	some species are present in both sites ($a > 0$) and richness change (b-c) is negative	if $a > 0$ and b-$c < 0$, then a+|b-c| if $a > 0$ and b-$c > 0$, then a if $a = 0$ or |b-c|=0, then 0	this paper
losing strict nestedness (=strict nestedness with species loss)	some species are present in both sites ($a > 0$) and richness change (b-c) is negative	if $a > 0$ and b-$c > 0$, then a+|b-c| if $a > 0$ and b-$c < 0$, then a if $a = 0$ or |b-c|=0, then 0	this paper

the temporal context (Legendre, 2019; Magurran et al., 2019). The Gain *PPC* contains species absent from the first sampling unit but present in the second one. In contrast, the Loss *PPC* includes species that are present in the first sampling unit but absent from the second one (Legendre, 2019). It is therefore clear that for a given pair of sampling units, Loss and Gain *PPCs* together represent community change. The example in Fig. 1 shows how the pattern of a pair of sampling units (pairwise pattern) corresponding to different positions, g_i and g_j along a gradient, can be divided into Overlap, Gain, and Loss *PPCs*.

As in Schmera et al. (2020); we argue here that *PPCs* reflect the individual or combined response types of a community to the underlying process along the gradient such as no effect (indicated by Overlap *PPC*), species gain (Gain *PPC*) and loss (Loss *PPC*). Moreover, like in non-directional analysis (Schmera et al., 2020) where Replacement and Richness difference *PPCs* together form beta diversity, for directional analysis beta diversity (=turnover) is the sum of the Gain and Loss *PPCs*.

We also suggest that Gain and Loss *PPCs* constitute *gaining, losing* and *neutral turnover* (Table 1). *Gaining turnover* refers to beta diversity dominated by gain, *losing turnover* to beta diversity dominated by loss, and *neutral turnover* to beta diversity with balanced gain and loss. The broad nestedness concept (note: nestedness may exist for equally rich sampling units, Podani and Schmera, 2012) can also be interpreted in directional analysis. Overlap *PPC* and the surplus of Gain *PPC* in relation to Loss *PPC* (see nestedness definition of Podani and Schmera, 2011) form together *gaining nestedness*, Overlap *PPC* and the surplus of Loss *PPC* in relation to Gain *PPC* constitute *losing nestedness*, while the sole existence of Overlap *PPC* can be regarded as *neutral nestedness* (that is, *similarity*). Finally, if nestedness is interpreted in the strict sense (i.e., nestedness does not exist for sampling units with equal species number, Podani and Schmera, 2012), then Overlap *PPC* and the surplus of Gain *PPC* in relation to Loss *PPC* form together *gaining strict nestedness* with the condition that the surplus exists (see strict nestedness definition of Podani and Schmera, 2011). Similarly, Overlap *PPC* and the surplus of Loss *PPC* in relation to Gain *PPC* produce *losing strict nestedness* (Table 1). These indices are computed from presence-absence species data.

2.2. Raw measures using the number of species

We follow the standard system of abbreviations used for pairwise comparisons (e.g. Koleff et al., 2003) and for measuring temporal beta diversity (Legendre, 2019). In this, a is the number of species present in both sampling units, b is the number of species present only in the first sampling unit and c is the number of species present only in the second one, so that $n = a + b + c$ is the number of species in the two sampling units combined. We suggest quantifying Overlap *PPC* by the number of shared species (a), Gain *PPC* by the number of species present only in the second sampling unit (c), and Loss *PPC* by the number of species present only in the first sampling unit (b). As seen from Table 1, we can also quantify the different concepts of turnover and nestedness.

2.3. Relativization by the number of species present in the two sampling units combined

To make the calculation independent of species richness, all measures described above are to be divided by n. This division normalizes all measures to the interval [0,1], which – if multiplied by 100 – can be interpreted in terms of percentages of the total species richness of the two sites being compared (Table 2). The relativized amount of overlap (hereafter relativized overlap) is identical to the well-known similarity coefficient (Jaccard, 1901). The other measures are novel because directional changes were rarely, if ever considered previously. Relativized turnover measures (i.e. relativized gaining turnover, relativized neutral turnover and relativized losing turnover) are based on Jaccard dissimilarity, while relativized nestedness measures (i.e. relativized gaining nestedness, relativized neutral nestedness, relativized losing nestedness, relativized strict gaining nestedness and relativized strict losing nestedness) follow the alternative nestedness concepts defined in Podani and Schmera (2011). As explained above; these new measures

Table 2

Concepts and the corresponding relativized measures for directional analysis of community change between two sampling units, quantified by the number of species and relativized by division by the Jaccard or the Sørensen index denominator. Abbreviation: $n = a + b + c$. References for measures: Ref.1 – (Jaccard, 1901); Ref.2 – (Sørensen, 1948); Ref.3 – (Legendre, 2019); Ref.4 – this paper.

Concept	Relativized measure with Jaccard denominator	Relativized measure with Sørensen denominator
overlap	a/n (Ref.1)	$2a/(2a + b + c)$ (Ref.2)
species gain	c/n (Ref.3)	$c/(2a + b + c)$ (Ref.3)
species loss	b/n (Ref.3)	$b/(2a + b + c)$ (Ref.3)
gaining turnover	if $c > b$ then $(b + c)/n$ else 2 min(b,c)/n (Ref.4)	if $c > b$ then $(b + c)/(2a + b + c)$ else 2 min(b,c)/$(2a + b + c)$ (Ref.4)
neutral turnover	2 min(b,c)/n (Ref.4)	2 min(b,c)/$(2a + b + c)$ (Ref.4)
losing turnover	if b > c then $(b + c)/n$ else 2 min(b,c)/n (Ref.4)	if $b > c$ then $(b + c)/(2a + b + c)$ else 2 min(b,c)/$(2a + b + c)$ (Ref.4)
gaining nestedness	if $a > 0$ and b-$c < 0$ then $(a+\|b\text{-}c\|)/n$ if $a > 0$ and b-$c \geq 0$ then a/n if $a = 0$ then 0 (Ref.4)	if $a > 0$ and b-$c < 0$ then $(2a+\|b\text{-}c\|)/(2a + b + c)$ if $a > 0$ and b-$c \geq 0$ then $2a/(2a + b + c)$ if $a = 0$ then 0 (Ref.4)
neutral nestedness	if $a > 0$ then a/n if $a = 0$ then 0 (Ref.4)	if $a > 0$ then $2a/(2a + b + c)$ if $a = 0$ then 0 (Ref.4)
losing nestedness	if $a > 0$ and b-$c > 0$ then $(a+\|b\text{-}c\|)/n$ if $a > 0$ and b-$c \leq 0$ then a/n if $a = 0$ then 0 (Ref.4)	if $a > 0$ and b-$c > 0$ then $(2a+\|b\text{-}c\|)/(2a + b + c)$ if $a > 0$ and b-$c \leq 0$ then $2a/(2a + b + c)$ if $a = 0$ then 0 (Ref.4)

gaining strict nestedness	if $a > 0$ and b-$c < 0$ then $(a+\|b\text{-}c\|)/n$
	if $a > 0$ and b-$c > 0$ then a/n
	if $a = 0$ or $\|b\text{-}c\|=0$ then 0 (Ref.4)
		if $a > 0$ and b-$c < 0$ then
		$(2a+\|b\text{-}c\|)/(2a + b + c)$
		if $a > 0$ and b-$c > 0$ then
		$2a/(2a + b + c)$
		if $a = 0$ or $\|b\text{-}c\|=0$ then 0 (Ref.4)

losing strict nestedness	if $a > 0$ and b-$c > 0$ then $(a+\|b\text{-}c\|)/n$
	if $a > 0$ and b-$c < 0$ then a/n
	if $a = 0$ or $\|b\text{-}c\|=0$ then 0 (Ref.4)
		if $a > 0$ and b-$c > 0$ then
		$(2a+\|b\text{-}c\|)/(2a + b + c)$
		if $a > 0$ and b-$c < 0$ then
		$2a/(2a + b + c)$
		if $a = 0$ or $\|b\text{-}c\|=0$ then 0 (Ref.4)

consider directional change in the community from one sampling unit to another along a gradient (Table 2). The entire approach, like the original SDR method, may be modified in a way that *PPCs* are expressed according to the Sørensen index (Table 2). Supplementary Document 2 provides an R function *directional.response* for computation of the new indices. This function is also available in R package *adespatial* (Dray et al., 2021).

3. Interpretation of the new measures

3.1. Comparison of raw and relativized measures

Our first toy matrix $\mathbf{A}_1$ is used to illustrate the difference between raw and relativized indices. $\mathbf{A}_1$ contains 3 sampling units (rows) and 6 species (columns). The cells of the matrix contain species presences (1) or absences (0):

$$\mathbf{A}_1 = \begin{bmatrix} 1 & 1 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}$$

The community pattern represented by $\mathbf{A}_1$ has been referred to as anti-nested pattern (Almeida-Neto et al., 2008; Podani and Schmera, 2011). We assume that the ecological gradient changes from sampling unit 1 (top row) through sampling unit 2 (middle row) to sampling unit 3 (bottom row). Losing turnover (Table 1) between site pairs 1 and 2, 2 and 3, and finally between 1 and 3 equals to 5, 4, and 3. These values indicate that 5, 4 and 3 species are involved and form losing turnover in pairwise comparisons. Principal coordinates analysis (PCoA, Legendre and Legendre, 2012) of the sampling units correctly represents the relatedness of the three sampling units (Fig. 2A). However, if relativized losing turnover with Jaccard or Sørensen denominator, then all three percentage distances will be 100%, suggesting that 100% of the species of each sampling unit pair show losing turnover. In that case, the PCoA ordination plot represents sampling units as an equilateral triangle (Fig. 2B). The analysis of $\mathbf{A}_1$ shows that raw measures (Table 1) quantify ecological phenomena in terms of the number of species, whereas relativized measures (Table 2) show the results as fractions of the total species richness of the two sampling units.

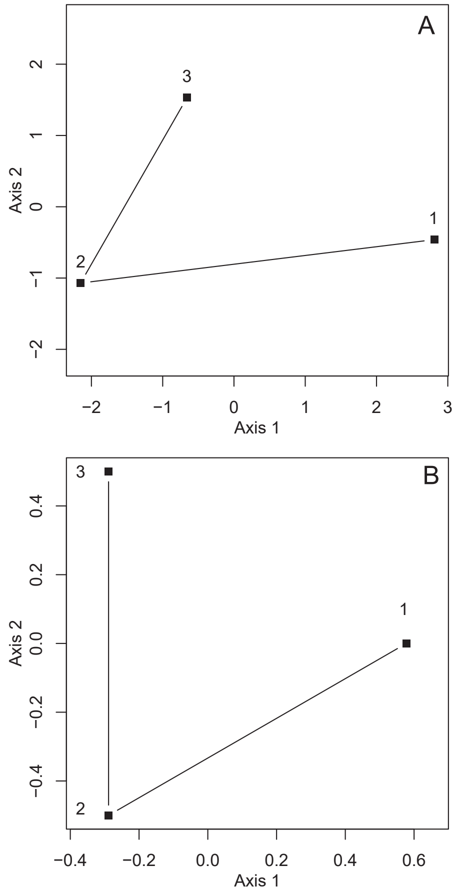

Fig. 2. Ordination plot of the three sampling units of $\mathbf{A}_1$ (numbers 1 to 3) by principal coordinates analysis (PCoA) using (A) losing turnover and (B) relativized losing turnover as distance. To emphasize the gradient, neighbouring sampling units are connected.

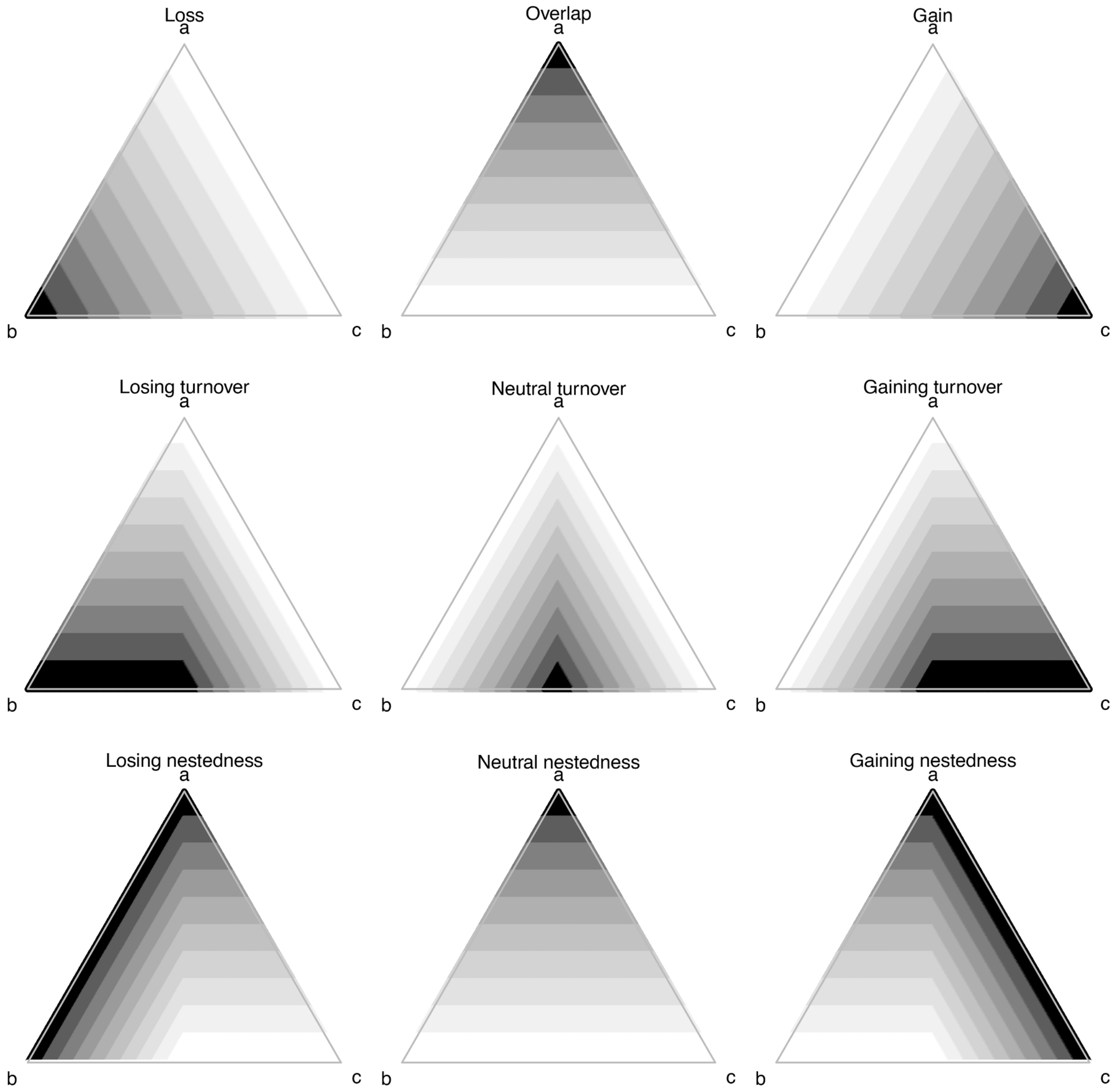

Fig. 3. Patterns of variation in the values of new relativized measures [shading on an equal interval scale, from low (white) to high (black)] for pairwise comparison between two hypothetical sampling units. a: number of species present in both sampling units, b: number of species present only in the first sampling unit, c: number of species present only in the second sampling unit. The degree of shading in each plot represents the value of the given measure (darker shading for larger values, lighter shading for smaller values). Shading is discretized following Koleff et al. (2003).

3.2. *Visual interpretation of relativized measures using ternary plots*

To interpret the behaviour of the new relativized pairwise measures, 200 species were distributed among three sets (overlap, loss and gain). We calculated the statistics for all possibilities for writing $a \geq 0$, $b \geq 0$ and $c \geq 0$ with the condition that their sum is 200. Easy arithmetic shows that we have $(201 \times 202)/2 = 20{,}301$ different possibilities. We used ternary plots (see Koleff et al., 2003 and Podani and Schmera, 2011 for interpretation) with *a, b* and *c* as corners to demonstrate the pattern of variation of these measures for the 20,301 cases (Fig. 3). For instance, overlap decreases continuously from the top corner towards the bottom edge when a diminishes (middle diagram, upper row, Fig. 3), whereas neutral nestedness is the maximum when $b = c$, and a is small, and decreases towards the right and the left edge (middle diagram, middle row, Fig. 3). It is easy to see that overlap, neutral turnover and neutral nestedness are directional regarding the number of species present only in the first (b) and second (c) sampling unit, while the other measures are non-directional. Loss, losing turnover and losing nestedness show sensitivity to the number of species present only in the first sampling unit (b), while gain, gaining turnover and gaining nestedness to the number of species present only in the second sampling unit (c).

3.3. *Comparison of directional and non-directional measures*

Our second toy matrix $\mathbf{A}_2$ is used to illuminate the difference between non-directional measures (e.g. relativized nestedness, Podani and Schmera, 2011; relativized neutral nestedness) and directional measures (relativized gaining nestedness, and relativized losing nestedness, Table 2).

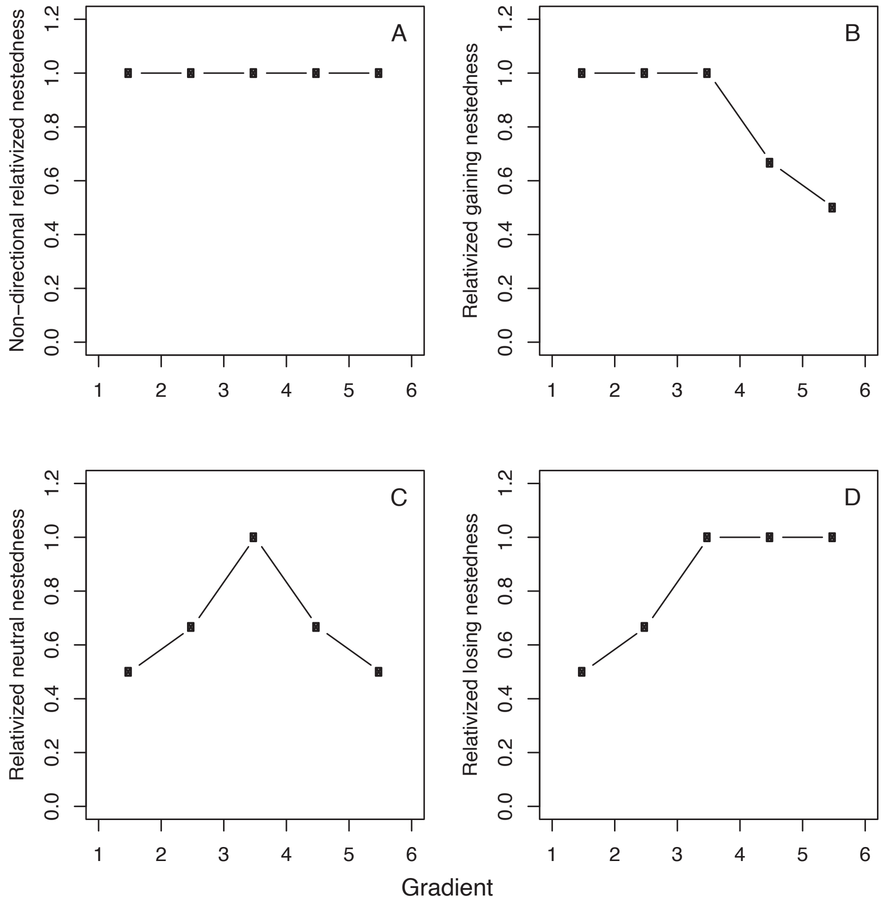

Fig. 4. The response of non-directional nestedness (N_{rel}, Podani and Schmera, 2011) (A), relativized gaining nestedness (B), relativized neutral nestedness (C) and relativized losing nestedness (D) measures to community changes in $\mathbf{A}_2$. Only neighbouring sampling units along the gradient were studied.

$$\mathbf{A}_2 = \begin{bmatrix} 1 & 0 & 0 \\ 1 & 1 & 0 \\ 1 & 1 & 1 \\ 1 & 1 & 1 \\ 1 & 1 & 0 \\ 1 & 0 & 0 \end{bmatrix}$$

$\mathbf{A}_2$ contains 6 sampling units so that the gradient studied runs from the first (top row of the matrix) to the last unit (bottom row of the matrix). Our analysis focuses on how nestedness changes from one sampling unit to the next along the gradient, i.e., we consider only neighbouring pairs of units. McGeoch et al. (2019), for instance, call this the nearest neighbour scheme. For 6 distinct sampling units, we have 5 neighbouring pairs, so that our analyses indicate 5 instances of change. The non-directional relativized nestedness (N_{rel}, Podani and Schmera, 2011) indicates 100% nestedness along the entire gradient (Fig. 4A). Relativized gaining nestedness show 100% nestedness for sampling unit pairs 1 and 2, 2 and 3, and finally for 3 and 4, and then relativized gaining nestedness decreases (Fig. 4B). Relativized neutral nestedness increases until sampling unit pair 3 and 4 (100%) and then decreases (Fig. 4C). Finally, relativized losing nestedness increases until sampling unit pair 3 and 4 (100%) and then remains constant (Fig. 4D). This example demonstrates that non-directional measures are not sensitive to directional changes in the community while our new directional measures do reflect directional changes.

3.4. Exercises for R users

We provide exercises to illustrate the interpretation of the new measures. In the first exercise (Suppl. Doc. 3), we simulate coenocline data and analyse them with our new directional measures. In the second example (Suppl. Doc. 4), we analyse the Doubs River fish data, a river in south-eastern France. Ecological interpretation of the results is also supplied in brief.

3.5. Recommendation for ecologists

As already noted, variation-type (*non-directional)* measures are inadequate for expressing *directional changes* in the community. They can, however, detect the importance (large values) of beta diversity (here we deliberately use the general term beta diversity instead of turnover) or nestedness among pairs of sites also in directional situations. This detection, however, requires further (directional) analyses, especially if multiple sites are studied along a gradient.

4. Analysis of actual data sets

We examine the performance of the new measures using four ecological data sets. The *Alpine snail* data set represents the community change of terrestrial gastropods within an elevational range from 1215 to 2550 m in Val Müstair, Switzerland. Sampling of snails was adopted to their activity and habitat use (Baur et al., 2014). The elevational gradient was divided into 9 bands (each covering a range of 150 m) and turnover and related measures among band level community data were

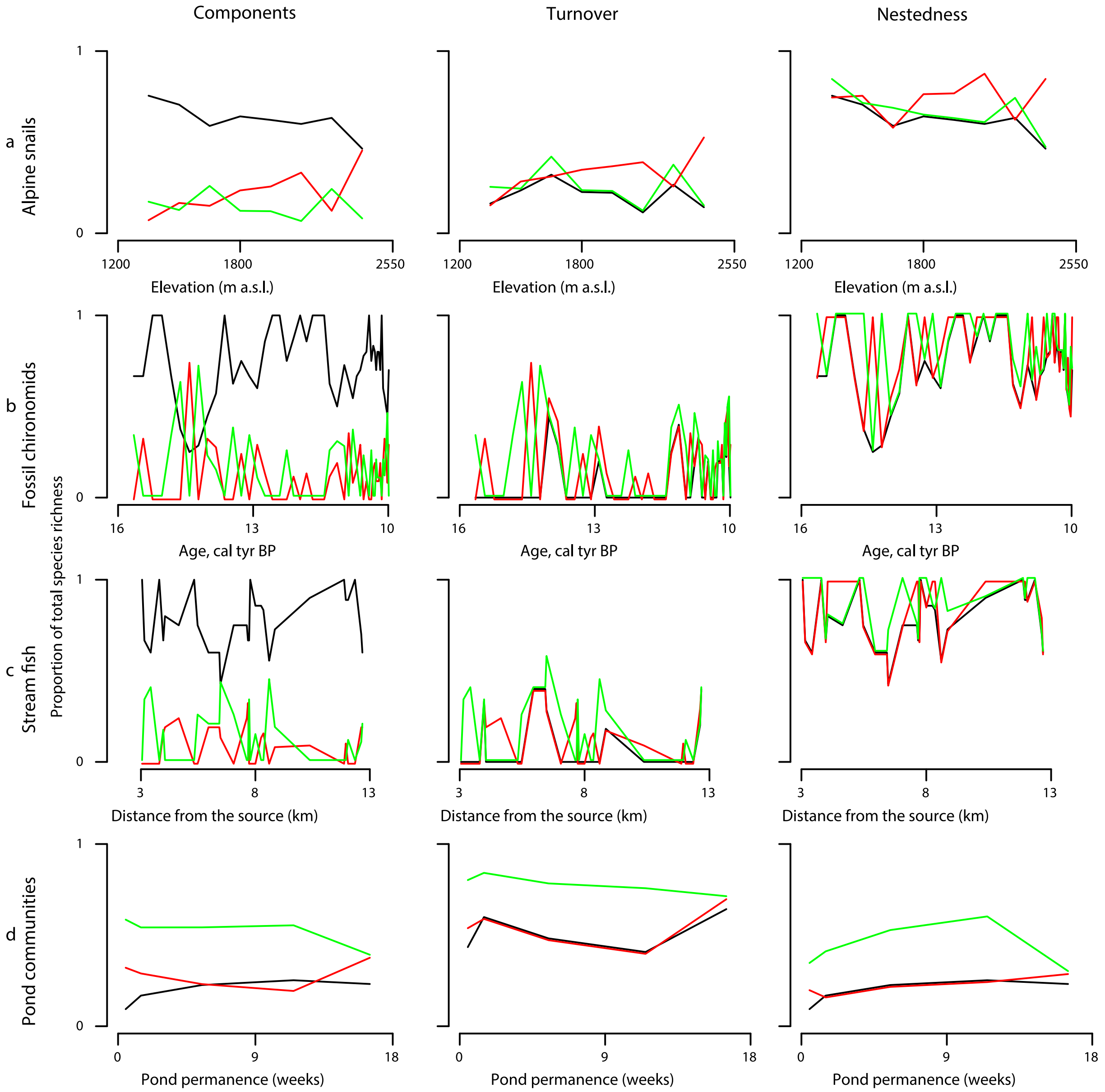

Fig. 5. The response of relativized measures to real ecological community changes. The horizontal axis of each plot shows an ecological gradient. Diagrams labelled on top as "Components" visualize overlap (black), species gain (green) and species loss (red), the "Turnover" diagrams include gaining turnover (green), neutral turnover (black) and losing turnover (red), while the "Nestedness" diagrams demonstrate gaining nestedness (green), neutral nestedness (black) and losing nestedness (red). Although community changes can only be interpreted at discrete positions along the gradient, we connected points for illustrative purposes. To support the recognition of overlapping values, we slightly shifted some values vertically. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

examined (Baur et al., 2014). The *Fossil chironomid* data set was obtained from the sediment of Lake Brazi, Retezat Mountains, Romania. Community changes in relation to the age of the sediment (expressed in years before present, hereafter yr BP) were analysed (Tóth et al., 2012). The *Stream fish* data set reflects the compositional changes of fish assemblages along a longitudinal gradient of the Bernecei–Kemence stream system, Börzsöny Mountains, Hungary. The fish fauna as well as the directed gradient distance from the source were recorded for each pool (Erős and Grossman, 2005). Finally, the *Pond community* data set contains the fauna (composed by invertebrates and amphibians) of temporary ponds in Connecticut, USA. Pond permanence was assessed as the number of weeks during which visible water was recorded after June and was related to community changes (Urban, 2004).

We applied relativized measures for a given pair of sampling units where relativization is based on the number of species present in the union of the two units (Table 2; this approach complies with the Jaccard index). Consequently, measures are expressed as the proportion of total species richness in the two sampling units combined. We examined the community change of neighbouring sampling units only. If the same gradient value was assigned to two or more sampling units (e.g., in the pond community data, four ponds had a permanence value of 0 weeks), then the average was calculated. In the figure, the resulting values are placed at the average gradient position of the neighbouring sampling units (Fig. 4).

The analysis of the *Alpine snail* data set reveals that the community is characterized mostly by overlap (Fig. 5a). The gain component is close to zero while the loss component increases with increasing elevation. The slight dominance of the loss component causes losing turnover and losing nestedness. The analysis of the *Fossil chironomid* data set reveals high overlap (>0.5) of the species composition of neighbouring sampling units (Fig. 5b), resulting in a moderate value of turnover (<0.5) and a high value of nestedness (>0.5). This means that when only presence/absence is considered, then the chironomid assemblages show relative stability (expressed by overlap) with age. In contrast to this high average value of overlap, the loss and gain components reflect remarkable community change between 15,000 and 14,000 yr BP. The analysis of the *Stream fish* data set demonstrates that the assemblage exhibits high degree of overlap (>0.5) along the longitudinal gradient of the stream (Fig. 5c). On average, the numerical value of gain is larger than the loss for neighbouring sampling units suggesting that increasing distance from the source promotes directional community change (Erős and Grossman, 2005). Our analyses also show that turnover is generally moderate (<0.5) and is dominated by gaining turnover. In addition, the stream fish assemblages exhibit gaining nested pattern (i.e. the average gaining nestedness measure is larger than the average losing nestedness) in response to increasing distances from the source. Finally, the analysis of *Pond community* reveals that the pattern is dominated by the gain component (Fig. 5d). This means that the community shows directional response to increasing pond permanence (Urban, 2004). There are gaining turnover in relation to increasing pond permanence and moderate gaining nestedness. In sum, our analyses demonstrate that actual communities do show directional community changes along the ecological gradient studied.

5. Discussion

Previously described methods of partitioning beta diversity into components focus exclusively on variation among the sites but analogous interpretation of multiple components of beta diversity along environmental, spatial, or temporal gradients require further work. We argued that the assessment of such changes should consider the positions of sampling units along the gradient to reflect the direction of community changes. In line with this requirement, we suggested here a method of partitioning turnover and developed a methodology to quantify several important directional aspects of community change — overlap, gain and loss — along a gradient.

The increasing need for quantifying the change of communities along gradients together with the finding that components of beta diversity can be used efficiently for revealing background mechanisms driving communities (Baselga, 2010) promoted the intensive use of beta diversity components in gradient analyses (Suppl. Doc. 1). We emphasize that components of beta diversity that simply quantify variation cannot reflect the response of the community to a directed gradient. Thus, they provide inadequate information on how a particular physical gradient influences the community.

Our methodology supplements the existing toolkit of community ecology by focusing on the position of sampling units along a gradient and by quantifying the directional community responses. Regarding the latter, we emphasized species losses and gains (Legendre, 2019; Magurran et al., 2019), and formulated different directional measures of turnover and nestedness following Podani and Schmera (2011) and Schmera et al. (2020). Since the new measures are sensitive to *directional* community changes; we distinguished among *gaining*; *losing* and *neutral* measures, based on the number of species, and showed how to relativize the new measures following the tradition of the Jaccard and Sørensen (dis)similarity indices to make them independent of the total number of species observed at the sites.

Although the term turnover is related by definition to directional community changes (Anderson et al., 2011), the connection of nestedness to a gradient is less straightforward. Atmar and Patterson (1993) viewed the order of species extinctions as highly deterministic; and called it as inherent orderliness of extinction patterns. They argued that the extinction of species on each island of an archipelago depends on fragmentation (i.e. on the size of the islands) and thus “each smaller island would contain only a proper subset of the species found on all larger islands”. Consequently, they proposed that a nested pattern reflects an orderly sequence of extinction on islands in relation to fragmentation. This idea popularized the concept of nestedness. Later, Almeida-Neto et al. (2008) argued that the isolation and the size of the habitat might explain the emergence of nestedness. According to these findings; nestedness should express a directional community change along a gradient. In their seminal review paper, however, Ulrich et al. (2009) decoupled ecological gradients and the concept of nestedness by saying: “In a nested pattern; the species composition of smaller assemblages is a nested subset of the species composition of larger assemblages”. Moreover, the frequently used nestedness measures (NODF, Almeida-Neto et al., 2008; N_{rel}, Podani and Schmera, 2011) do not consider any gradient. Consequently, the existing methodology is inadequate to connect nestedness to a gradient, even though there is a clear need for this.

The methodology we suggested here fills this gap and allows researchers to quantify the *directional response* of the community to a gradient. Similarly to the approaches focusing on variation-type beta diversity, we paid special attention to the relationship between beta diversity and nestedness. Analyses of actual data sets showed that communities may exhibit nestedness (alpine snails, fossil chironomids, stream fish) or turnover (pond communities) along a gradient, even though these two phenomena are not mutually exclusive. Compared to the variation-based community analyses, we identified directional patterns using directional measures. For instance, the alpine snail communities were dominated by loss (and losing nestedness) in relation to increasing elevation, whereas the pond communities were dominated by gain (and gaining turnover) as a response to increasing permanence. Such inferences reveal an unexplored aspect of community organisation.

Our conclusions depend not only on the measures used, but also on the choice of sampling units to be compared. Here we analysed and discussed data for neighbouring pairs of sampling units only for actual data sets. Obviously, it may also be meaningful to compare community response with reference to the first sampling unit (e.g. Fig. 3 in Legendre and Salvat, 2015; Fig. 3 in Legendre, 2019; and Fig. 2 in Magurran et al., 2019), called the “fixed-point origin” design (McGeoch et al., 2019). To provide a universal tool for ecologists, our R function *directional.response* (Suppl. Doc 2) examines each pair of sampling sites, thereby allowing different designs to be considered. It is important to note that even a carefully selected measure combined with an appropriate sampling design cannot guarantee an unbiased conclusion. This is because inferences from community patterns depend not only on the analytical aspect of the methodology (measure and design), but also on the adequacy of the sampling strategy. As the field sampling of ecological communities is challenging (Czeglédi et al., 2021) and influenced by imperfect species detection (Hamer et al., 2021), the sampling procedure might result in a biased presence-absence matrix. The most likely bias is that species are not detected even when they are present in a study site. To avoid such sampling bias, special attention should be paid to the representativeness, comparability and reliability of samples (Cao et al., 2002; Ramsey and Hewitt, 2005).

In sum, we extended the mathematical toolkit of numerical ecology to assess the directional change of community if there is an underlying ecological gradient. We showed that – similarly to the variation-based decomposition of beta diversity – it is possible to decompose beta diversity into directional components. These components, combined with others, allow the quantification of different concepts of ecology, such as turnover and nestedness.

Author contributions

DS, PL and JP conceived the idea, TE, MT, EKM and BB collected the data, DS and PL analysed the data, DS, JP and PL led the writing of the manuscript. All authors contributed to the interpretation of the results as well as to the manuscript drafts.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2022.108618.

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