

What do beta diversity components reveal from presence-absence community data? Let us connect every indicator to an indicandum!



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ARTICLE INFO

Keywords:

Beta diversity partitioning
Community pattern
Nestedness
Pairwise pattern components
Replacement
Richness difference

ABSTRACT

Extracting meaningful information from community data is among the most challenging tasks of community ecology. Whereas presence-absence data matrices are commonly used in different analytical frameworks, we argue that the conceptual distinction among community patterns (on which inference is made), pairwise pattern components (PPCs, which reflect the unique response of communities for pairs of sites), and measures (which quantify a relevant property of PPCs), liberates our field from the possible misinterpretation of results derived from existing approaches. The novel concept suggested here is the PPC, which can be efficiently used to identify response types of communities, thereby shortening the list of potential explanatory processes. Consequently, the introduction of PPCs supports the analysis of real data sets and links patterns to ecological hypotheses. Based on PPCs, we proposed a new partitioning of beta diversity (SET framework) into intersection (*I*) of nestedness and beta diversity and the relative complement (*RC*) of nestedness in beta diversity. We performed an algebraic assessment of three existing partitioning frameworks of beta diversity: the BAS (Baselga, 2010, Global Ecology and Biogeography), POD (Podani and Schmera, 2011 Oikos) and SET (present paper). We found that when a community pattern is anti-nested, which is characterized by the presence of both Replacement and Richness difference PPCs, the BAS framework falsely indicates a 100% share of replacement from beta diversity. In contrast, the POD and SET partitioning procedures detect the presence and the proper size of PPCs for all types of community patterns. In conclusion, we argue that breaking down community patterns into PPCs and then quantifying the importance of these PPCs form a straightforward strategy to extract information from community data under a broad range of circumstances.

1. Introduction

Most commonly, field sampling provides sites-by-species co-occurrence (presence-absence) data matrices. We consider such matrices as representations (or images, Wildi, 2017) of real sampled communities and refer to them as *community patterns* for simplicity. Extracting meaningful information from community patterns is among the most challenging tasks of community ecology (Morin, 2011). Pioneers of ecology inferred the existence of structuring forces from the community patterns observed (e.g. Clements, 1916; Gleason, 1926). Some of these community patterns have received particular attention and are called now as idealized community patterns (Almeida-Neto et al., 2008; Carvalho et al., 2013; Ulrich and Gotelli, 2013). Notably, some of these idealized community patterns do not differ from each other if the ordering of sites and species is disregarded (e.g. the checkerboard pattern

is equivalent to compartment pattern, Podani and Schmera, 2011), while another group of patterns can only be interpreted along a gradient (i.e. when the order of sites is defined), such as the perfect gradient (Podani and Schmera, 2011) as well as Clementsian, Gleasonian and evenly spaced patterns (Schmera et al., 2018). To avoid these challenges, here we focus only on community patterns that are insensitive to the ordering of sites and species in the data matrix. However, the remaining idealized community patterns cannot unambiguously be used to reveal background processes. Ulrich et al. (2009) showed, for instance, that nestedness, i.e. the ordered subset relationship in the species composition of survey sites, can result from multiple processes related to selection, drift and dispersal. Consequently, numerical ecology is not in the position to link patterns to underlying processes unambiguously.

Notwithstanding the complexity of the problem, community

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<https://doi.org/10.1016/j.ecolind.2020.106540>

Received 17 September 2019; Received in revised form 2 April 2020; Accepted 14 May 2020

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patterns are generally evaluated by simple indicators that express fundamental phenomena by a single number. Beta diversity, as suggested by Whittaker (1960) and expanded later (Legendre et al., 2005; Anderson et al., 2006) reflects community differentiation. Baselga (2010) recognized that beta diversity may be decomposed into fractions, which can then be associated with different ecological phenomena. He suggested that beta diversity of pairs of sites be subdivided into replacement (his original term was “turnover”) and “nestedness-resultant” components. Species replacement refers to a well-known fact that species tend to substitute one another along ecological coenoclines (Whittaker, 1972) while the nestedness-resultant component refers to the fraction of beta diversity caused by nestedness (Baselga, 2010). This procedure, called BAS partitioning (Legendre, 2014), is considered a major contribution to the field of community ecology because the components depict unique phenomena, which are assumed to reflect the existence of different underlying mechanisms driving beta diversity. Thanks to its novelty and soundness, this framework has triggered a fruitful exchange of ideas, which led to further methodological developments (Almeida-Neto et al., 2012; Baselga, 2012; Baselga and Leprieur, 2015; Carvalho et al., 2013; Podani and Schmera, 2011, 2016; Schmera and Podani, 2011). An alternative method separates the total (gamma) diversity of pairs of sites into similarity, relativized replacement and relativized richness difference components (SDR-simplex method, Podani and Schmera, 2011). SDR stands for Similarity, richness Difference, and Replacement, the three variables used to draw the simplex plot, which is a triangular graph (Podani and Schmera, 2011). According to this methodology, relativized replacement and richness difference components form together the relativized beta diversity (Cardoso et al., 2009, 2014; Carvalho et al., 2013; Podani and Schmera, 2011), and therefore it can also be regarded as beta diversity partitioning (POD framework, Legendre, 2014). Independently of the partitioning applied, components of beta diversity are considered to reveal unique community components and are frequently used to improve our understanding of crucial geographical, ecological and conservation issues. These include, for instance, the response of communities to elevation gradients (Marini et al., 2013) or to climate change (Lewis et al., 2016).

The present paper is focused on what beta diversity components indicate about community patterns. The key contribution is the introduction of pairwise pattern components which (1) reflect the unique response of communities, (2) refer to well-known ecological concepts, (3) allow the classification of natural community patterns, and (4) provide a conceptual basis for a novel partitioning of beta diversity. We argue that breaking down community patterns to well-interpretable “building blocks” and followed by quantification of these building blocks and structural components derived as their combinations should be a sound and straightforward strategy to support inference about communities. To do this in an operative way, we propose that a conceptual distinction be made among *community patterns* (i.e. the objects on which inference is made) and the *pairwise pattern components* (PPCs, which are the building blocks of community patterns reflecting unique responses of communities). Each building block represents a phenomenon or concept to be indicated or recognized, called an *indicandum* (plural: *indicanda*). And finally the *measures*, called *indicators*, quantify relevant properties of PPCs. The novel concept suggested here is the *pairwise pattern component*, which was implicit in the approaches of Podani and

Schmera (2011) and Legendre (2014) but remained less clearly distinct from overall community patterns (e.g. perfect nested pattern or anti-nested pattern) and from measures (e.g. a particular coefficient of species replacement or nestedness). We feel that this gap is a continuous source of misinterpretation of results derived from the application of these approaches.

As a remedy, first we show that PPCs reflect unique responses of communities; therefore, identifying them is a significant and well-interpretable step in community analysis. We illustrate also that certain pairs of PPCs correspond to ecologically meaningful concepts such as beta diversity and nestedness. We outline a classification of published idealized community patterns based on contributions of PPCs and show that the measures constituting the SDR-simplex (Podani and Schmera, 2011) adequately quantify the above-mentioned concepts in any presence-absence based community pattern. The increasing need for quantifying the nestedness-related component of beta diversity motivated us to suggest a new scheme for beta diversity partitioning. The new framework, hereafter referred to as the SET framework (referring to set theory) in order to distinguish it from BAS and POD, decomposes beta diversity of pairs of sites into the intersection (*I*) of nestedness and beta diversity and the relative complement (*RC*) of nestedness in beta diversity components. More specifically, the SET framework examines how PPCs form sets of PPCs conceptualizing nestedness and beta diversity. Then, based on set theory, it quantifies the intersection and the relative complement of these elements. Obviously, the intersection of nestedness and beta diversity is related to nestedness, whereas the relative complement of nestedness in beta diversity is the remaining (nestedness-unrelated) component of beta diversity. Then, we overview existing partitioning methods by considering PPCs. Specifically, using algebraic approaches and analysing an actual data set, we examine whether a given component of different beta diversity partitions (the indicator) can explicitly indicate PPCs and derived ecological concepts (indicandum) in different community patterns. We inspect, for instance, whether the different components of beta diversity (indicators) indicate replacement (indicandum) or the joint fraction of nestedness and beta diversity (another indicandum). We find, for example, that in case of anti-nested patterns (i.e. if the community pattern contains both Richness difference and Replacement PPCs while the Overlap PPC is absent), the BAS framework falsely indicates 100% replacement, thus overestimating the Replacement PPC. We discuss the consequences of this finding and argue that the careful selection of indicators is not an irrelevant detail, but a basic component of an accurate community analysis.

2. Distinction among pairwise pattern components, community patterns and measures

2.1. Pairwise pattern components (PPCs) and derived concepts

We suggest that the effect of any process shaping presence-absence matrices can manifest itself through three PPCs or their combinations (we use capitalized names; Table 1; Fig. 1). Accordingly, PPCs reveal whether the underlying process has no effect (indicated by *Overlap*), it changes composition (*Replacement*), or modifies species richness (*Richness difference*, see the interpretation of these terms in more details in Podani and Schmera, 2011; Carvalho et al., 2012, 2013; Legendre,

Table 1
Description of the three pairwise pattern components (PPCs).

Pairwise pattern component	Description
Overlap	This is the similarity (<i>S</i>) component in the comparison of two community data vectors. It implies that some species are present in both sites. Overlap is caused by shared species (Podani and Schmera, 2011) or in other words by overlapping species (Schmera, 2017).
Replacement	This component is the first part of the dissimilarity (<i>D</i>) between two observations. It implies that a given number of species disappear in the first site and the same number of species appear in the second site.
Richness difference	This component is the second part of the dissimilarity (<i>D</i>) between two observations. It implies that the two sites are not equal in species number.

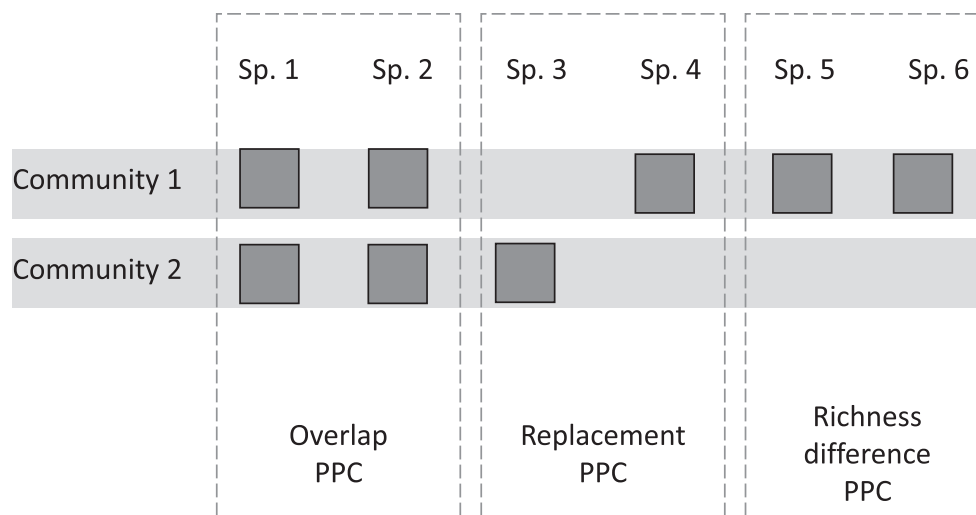


Fig. 1. Schematic representation of pairwise pattern components (Overlap, Replacement, and Richness difference).

2014). We argue that identifying such response types through PPCs supports inference about communities, because the identified response type might shorten the list of potential background effects. For instance, if a process changes species richness only, then Richness difference is the only PPC that indicates this effect.

Factors affecting community structure rarely occur individually in actual communities; response types are mostly present in pairs (or in triplets). Overlap and Replacement PPCs together constitute the concept of richness agreement (Podani and Schmera, 2011), while Replacement and Richness difference PPCs reflect the concept of community differentiation or, in other words, beta diversity (Whittaker, 1960; Anderson et al., 2011). The third and probably the most complicated concept that can be derived from pairs of PPCs is nestedness which refers to the subset relationship of sites (Ulrich et al., 2009). In examining the concept of nestedness of pairs of sites, some authors argue that nestedness exists only if the species composition of the two sites shows a proper (or strict) subset relationship (strict sense nestedness) while others reason for a broad-sense subset relationship (broad sense nestedness; see review for pairwise situations in Podani and Schmera, 2012). Here we apply both nestedness concepts (Wright et al., 1997; Almeida-Neto et al., 2008; Podani and Schmera, 2011) and define them as the Overlap and Richness difference PPCs taken together, with the condition that neither form of nestedness exists if the Overlap PPC is absent. In the broad sense version, nestedness exists even if the Richness difference PPC is absent. In the strict sense, nestedness exists only if both Overlap and the Richness difference PPCs are present. It is important to emphasize that until now we have discussed only the building blocks of communities (PPCs) and related concepts, but neither the patterns themselves nor the measures of any phenomenon.

2.2. Community patterns and their new classification

Community patterns are regarded as whole entities on which inference is made. The consequence of this is that the term community pattern (e.g. nested pattern, see Almeida-Neto et al., 2008; Podani and Schmera, 2011) should clearly be separated from concepts derived from PPCs (e.g. nestedness, see Podani and Schmera, 2012; Ulrich and Almeida-Neto, 2012). While the former refers to the whole entity, which might have specific properties (such as nestedness), the latter represents a specific property that may also characterize many other community patterns. For example, nestedness is a necessary constituent of a nested community pattern, but it may be present elsewhere as well (e.g. in a random pattern, Podani and Schmera, 2011).

Here we suggest a classification of community patterns (represented

by model presence-absence data matrices), which are insensitive to the ordering of sites and species (Table 2). The classification is based on PPCs and includes 11 patterns: *overlap*, *replacement*, *perfect richness agreement*, *compartment*, *perfect nested*, *minimum fill nested*, *maximum fill nested*, *anti-nested*, *beta diversity*, *perfect complex* and *complex*, such that impossible or ecologically irrelevant cases are excluded (e.g. richness difference alone appears only if one site contains species and the others are empty). Most of them are known from the literature; the 4 newly recognized ones are *overlap*, *perfect richness agreement*, *perfect complex* and *complex* patterns. The *Overlap pattern* refers to a situation in which all sites contain the same species, the *perfect richness agreement pattern* to a presence-absence matrix in which every pair of sites contains Overlap and Replacement PPCs, the *perfect complex pattern* to a presence-absence matrix in which every pair of sites contains all three PPCs, while the *complex pattern* refers to a presence-absence matrix in which all the three PPCs are present albeit not in every pair of sites. The term *beta diversity pattern* has been used by Almeida-Neto et al. (2008) with reference to a situation considered here as a replacement pattern (second row, Table 2). According to our interpretation, however, the *beta diversity* and *anti-nested patterns* contain both Replacement and Richness difference PPCs. The difference between these two is that in the *anti-nested pattern*, both PPCs are present in every pair of sites, which is not so in the *beta diversity pattern*. Consequently, these definitions correspond to the (meta-) community patterns described in Almeida-Neto et al. (2008), Podani and Schmera (2011), Ulrich and Gotelli (2013) and Schmera et al. (2018) with the note that these community patterns are now linked to PPCs. Most observed presence-absence data matrices belong to the complex pattern.

2.3. Measures

Ecological indication theory calls the phenomenon to be indicated as *indicandum*, while the measures quantifying relevant properties of the *indicandum* are the *indicators* (Heink and Kowarik, 2010). PPCs indicate unique response types while measures are expected to quantify relevant properties of PPCs. However, what is the distinguishing property characterizing each PPC (Fig. 1)? A simple and logical idea is that PPCs should be characterized by the number of constituting species. For example, Overlap, Replacement and Richness difference PPCs in Fig. 1 equally imply two species, while richness agreement (Overlap and Replacement PPCs together), beta diversity (Replacement and Richness difference PPCs together) and nestedness (Overlap and Richness difference PPCs together) each comprise four species. These measures are in fact the absolute components of the SDR-simplex method

Table 2

Classification of community patterns based on (1) the presence of *PPCs* [rows] and (2) whether the particular *PPCs* are present in each pair of sites [columns]. NA = not applicable. Rows are sites while species are columns in presence-absence model matrices. “1” = presence, “.” = absence.

Composition based on <i>PPCs</i>	Are the particular <i>PPCs</i> present in every pair of sites?	
	yes	No
only Overlap <i>PPC</i>	overlap pattern ¹ 1 1 1 1 1 1 1 1 1	NA
only Replacement <i>PPC</i>	replacement pattern ³ 1 1 1 1 1 1	NA
only Richness difference <i>PPC</i>	NA	NA
only Overlap & Replacement <i>PPCs</i>	perfect richness agreement pattern ¹	compartment pattern ^{2,3}
	1 1 . 1 . 1 1 1 1 . 1 1 1 1 1 .	1 1 . . 1 1 1 1 . . 1 1
only Overlap and Richness difference <i>PPCs</i>	perfect nested pattern ^{2,3}	minimum fill nested pattern ^{2,3} 1 1 1 1 1 . . . 1 . . . 1 . . . maximum fill nested pattern ^{2,3} 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 .
only Replacement and Richness difference <i>PPCs</i>	anti-nested pattern ³	beta diversity pattern ⁴
	1 1 1 1 1 1	1 1 1 1 1
Overlap, Replacement and Richness Difference <i>PPCs</i>	perfect complex pattern ¹	complex pattern ¹
	1 1 1 1 . 1 1 . . 1 . . . 1 1	1 1 1 1 . 1 1 . . 1 . . 1 1 1

¹This paper.²Almeida-Neto et al. (2008).³Podani and Schmera (2011).⁴The term was originally used in Almeida-Neto et al. (2008) to describe replacement pattern. Here we restrict its use to patterns which contain only Replacement and Richness Difference *PPCs* but these *PPCs* are not necessarily present in every pair of sites.

(Supplementary Table 1, SDR_{WB} , Podani and Schmera, 2011) and are expressed as the number of species forming PPCs and derived ecological concepts.

If PPCs and ecological concepts are quantified by the relative number of species and relativization is made by the total number of species present in the two sites, then these indicators are known as the Jaccard-type relativized measures of the SDR-simplex method (Supplementary Table 1, SDR_J , Podani and Schmera, 2011). Recently, Carvalho et al. (2012) and Legendre (2014) suggested that the Sørensen dissimilarity can also be decomposed into replacement and richness difference components. These components together with the Sørensen similarity can also be used as indicators. In this case, PPCs and related concepts are quantified by the number of presences divided by the sum of the presences in the two sites (Supplementary Table 1, SDR_S). Finally, following the idea of the Sørensen index, it is possible to quantify PPCs and concepts simply by the raw number of presences (Supplementary Table 1, SDR_{pres}).

In sum, indices suggested by Podani and Schmera (2011, 2016), Carvalho et al. (2013) and Legendre (2014) are indicators of PPCs and derived ecological concepts in any community pattern occurring in nature. They differ only in the quantification of the PPCs (i.e. quantified by number of species or presences), and whether this quantification is expressed by an absolute or relativized measure (Supplementary Table 1).

3. Introduction to the SET partitioning framework

Recently, there has been growing interest in partitioning beta diversity into nestedness-related and nestedness-unrelated components. To date, these two can only be separated by Baselga's (2010, 2012) methodology, called the BAS framework (Legendre, 2014). Here we suggest an alternative partitioning called the SET partitioning framework which follows the logic of PPCs.

This relies on PPCs and complies with both definitions of nestedness. If nestedness is interpreted in a broad sense, and if both Overlap and Richness difference PPCs are present, then the Richness difference PPC is the nestedness-related fraction of beta diversity (Fig. 2). If Overlap PPC is absent and thus no nestedness exists, then the Richness difference PPC pertains only to beta diversity. This means that beta diversity has no nestedness-related fraction (Fig. 2). Finally, if Richness difference PPC is not present, then beta diversity has no nestedness-related component (Fig. 2). The use of strict nestedness results in similar conclusions (Supp. Fig. 1).

Following this logic (Fig. 2) and based on set theory, the SET framework partitions beta diversity into the *intersection* (I) of nestedness and beta diversity and the *relative complement* (RC) of nestedness in beta diversity, where I stands for the nestedness-related component of beta diversity. Note that the SET partitioning results in the same outcome when nestedness is interpreted in either way, because if Overlap PPC exists but Richness difference PPC does not, then 1) nestedness does not exist and thus beta diversity and nestedness have no intersection (for strict nestedness), or 2) nestedness exists but the intersection of nestedness and beta diversity is zero (for broad sense nestedness; see Suppl. Fig. 1). For simplicity, here we deal only with broad nestedness. First, we introduce the notations, and then define beta diversity and nestedness, and finally the I and RC components of beta diversity. As the methodology has been developed for pairs of sites, we apply the notations of the 2×2 contingency table, with $n = a + b + c$ as the total number of species present in the union of the two sites. The number of unique species ($b + c$) explains compositional differentiation (or beta diversity, see Whittaker 1960), while the number of shared species (a) relates to compositional similarity (Jost et al., 2011). Regarding compositional differentiation, Weiher and Boylen defined beta diversity as $\beta_{WB} = b + c$ (Weiher and Boylen, 1994; Koleff et al., 2003), which can be decomposed into absolute species replacement $2 \min(b, c)$ and absolute richness difference $|b - c|$ (Podani and Schmera, 2011; Schmera

and Podani, 2011; Carvalho et al., 2012, 2013):

$$\beta_{WB} = b + c = 2 \min(b, c) + |b - c| \quad (1)$$

Podani and Schmera (2011) suggested measuring broad-sense nestedness (N) in the following way:

$$N = \begin{cases} a + |b - c| & \text{if } a > 0 \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

Now we examine the intersection of Weiher-Boylen diversity (β_{WB}) and nestedness (N) and the relative complement of nestedness in Weiher-Boylen diversity. Since the definition of nestedness includes a condition ($a > 0$), derivation is easier in two steps. If $a > 0$, then the intersection of nestedness and beta diversity is $|b - c|$ (if $b = c$ then $|b - c| = 0$ and if $b \neq c$ then $|b - c| > 0$), while the relative complement of nestedness in beta diversity is $2 \min(b, c)$:

$$b + c = |b - c| + 2 \min(b, c) \quad (3)$$

If $a = 0$, then $N = 0$, and therefore the intersection equals 0, while the relative complement is $b + c$ (the Weiher-Boylen diversity):

$$b + c = 0 + (b + c) \quad (4)$$

More generally, the Weiher-Boylen diversity (β_{WB}) can be partitioned into intersection (I_{WB}) and relative complement (RC_{WB}) components:

$$\beta_{WB} = I_{WB} + RC_{WB} \quad (5)$$

where

$$I_{WB} = \begin{cases} |b - c| & \text{if } a > 0 \\ 0 & \text{otherwise} \end{cases} \quad (6)$$

and

$$RC_{WB} = \begin{cases} 2 \min(b, c) & \text{if } a > 0 \\ b + c & \text{otherwise} \end{cases} \quad (7)$$

Note that if PPCs are characterized based on the number of presences then we will get similar equations (not shown here). In order to make the calculation independent of the total number of species present at the two sites, the fractions mentioned above are to be divided by n . The new components are termed Jaccard dissimilarity (D_J , Jaccard, 1912), intersection (I_J) and relative complement (RC_J), where subscript J refers to the Jaccard index:

$$D_J = I_J + RC_J \quad (8)$$

where

$$I_J = \begin{cases} |b - c| / (a + b + c) & \text{if } a > 0 \\ 0 & \text{otherwise} \end{cases} \quad (9)$$

and

$$RC_J = \begin{cases} 2 \min(b, c) / (a + b + c) & \text{if } a > 0 \\ (b + c) / (a + b + c) & \text{otherwise} \end{cases} \quad (10)$$

I_J was previously described as the “diversity-nestedness intersection coefficient” in Schmera and Podani (2011).

Finally, it is possible to apply this partitioning to the Sørensen dissimilarity (D_S , Sørensen, 1948) as well. In this case, intersection (I_S) and relative complement (RC_S) components take the following form:

$$D_S = I_S + RC_S \quad (11)$$

where

$$I_S = \begin{cases} |b - c| / (2a + b + c) & \text{if } a > 0 \\ 0 & \text{otherwise} \end{cases} \quad (12)$$

and

$$RC_S = \begin{cases} 2 \min(b, c) / (2a + b + c) & \text{if } a > 0 \\ (b + c) / (2a + b + c) & \text{otherwise} \end{cases} \quad (13)$$

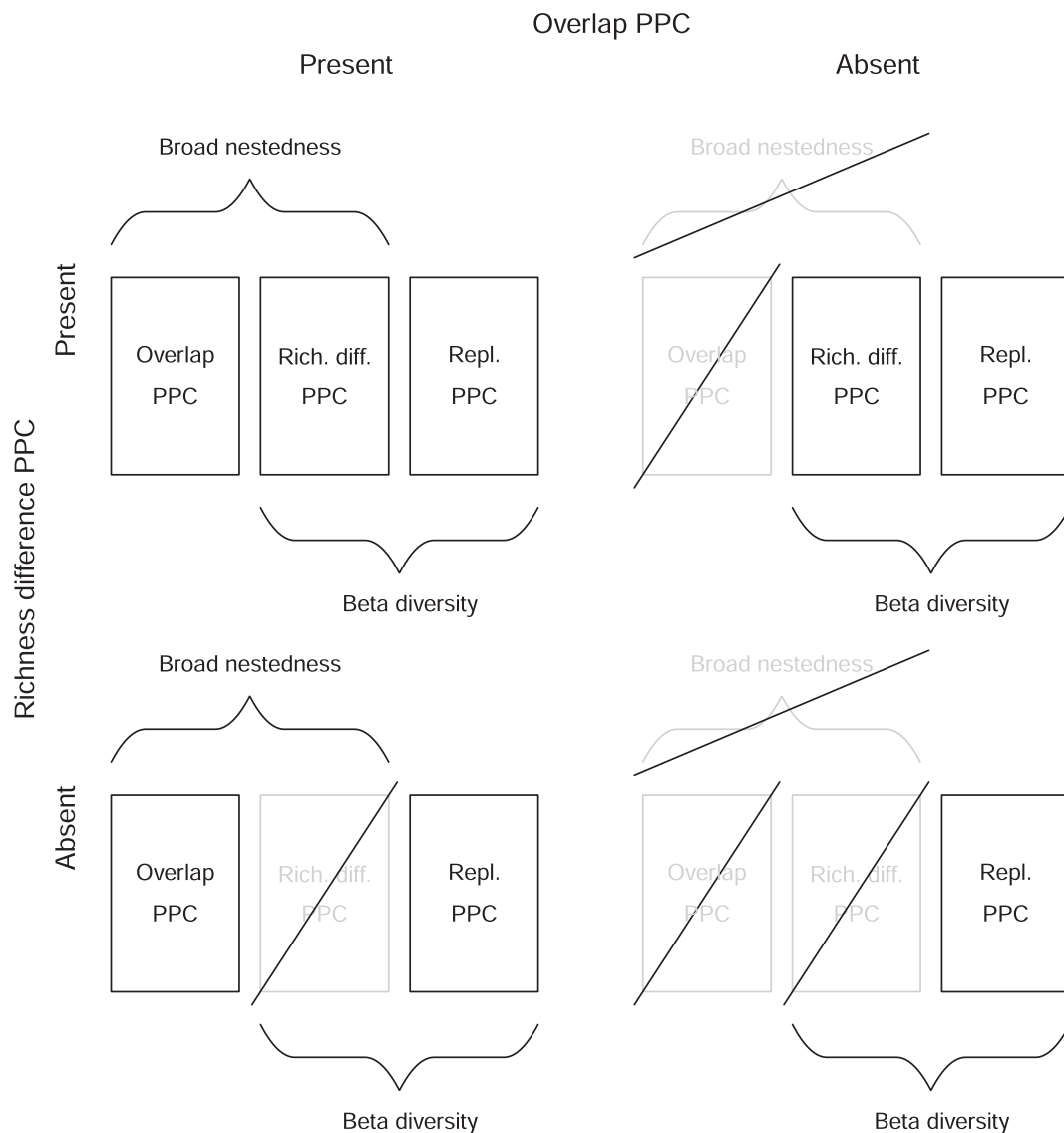


Fig. 2. A schematic representation of how the Richness Difference PPC can be interpreted as the nestedness-related fraction of beta diversity, depending on the presence and absence of Overlap and Richness difference PPCs, when nestedness is interpreted in a broad sense (Broad nestedness). Rich. diff. = Richness difference, Repl. = Replacement.

In sum, we provided a conceptual framework (SET partitioning framework) that partitions beta diversity into intersection of nestedness and beta diversity (I) and relative complement of nestedness in beta diversity (RC) components. This partitioning allows one to identify the importance of nestedness in beta diversity pattern through the I component. We provided the partitioning of three widely used beta diversity measures: the Weiher-Boyle diversity (β_{WB}), the Jaccard dissimilarity (D_J) and the Sørensen dissimilarity (D_S). The difference among them is that β_{WB} and its components (I_{WB} and RC_{WB}) use absolute (raw) values, D_J and its components (I_J and RC_J) are relativized by the number of species present in both sites, while D_S and its components (I_S and RC_S) are relativized by the average number of species present in both sites. These partitions imply that if the first component of beta diversity (I) is related to nestedness, then the second component can only be termed “remaining fraction” of beta diversity rather than replacement. [Supplementary Appendix 1](#) provides R scripts for the calculation of I and RC .

All of these suggest that POD and SET partitioning frameworks are similar because both partition beta diversity into components and both rely on PPCs. The difference between them stems from the phenomenon they reflect. The components of the POD framework illustrate the

ecological concepts of replacement and richness difference. These concepts are *directly* manifested by the Replacement and Richness difference PPCs, thus their quantification is straightforward. In contrast, the SET framework reflects the intersection of nestedness and beta diversity and the relative complement of nestedness in beta diversity. These concepts, however, are manifested by the Replacement and Richness difference PPCs in context-dependent way, due to the *complex nature of the ecological definition of nestedness*. Consequently, the SET partitioning framework is a novel partitioning of beta diversity, which is clearly different from the POD framework.

4. Comparison of different partitioning frameworks

4.1. Conceptual basis of the different frameworks

[Harrison et al. \(1992\)](#), [Williams \(1996\)](#) and [Lennon et al. \(2001\)](#) pioneered the idea that dissimilarity among communities results from replacement and species loss due to nestedness. [Baselga \(2010, 2012\)](#) formalized this by partitioning the Sørensen and the Jaccard dissimilarities into replacement and nestedness-related components (the latter was described by him as the nestedness resultant component, [Suppl.](#)

Table 2). The method was called the BAS partitioning framework (Suppl. Table 2, Legendre, 2014). An alternative partitioning (POD) framework, Podani and Schmera, 2011; Carvalho et al., 2012, 2013; Legendre, 2014 suggests that beta diversity can be decomposed into replacement and richness difference components. This idea has been formalized for the Weiher-Boylen diversity (Podani and Schmera, 2011), and for the Jaccard (Podani and Schmera, 2011) and Sørensen dissimilarities (Legendre, 2014, see Suppl. Table 2).

Legendre (2014) reviewed the meaning and the interpretation of the components of both approaches. He found that the two frameworks (BAS and POD) are complementary but further work was required to clarify the precise meaning of the different forms and to identify the domains of their application. Legendre's review revealed that the nestedness-related component of the BAS framework ("nestedness-resultant" component) and the richness difference component of the POD framework are intended to reflect different ecological concepts. In a more recent paper, Baselga and Leprieur (2015) concluded that if both approaches additively partition the same index (e.g. the Jaccard dissimilarity) and if the nestedness-related and richness difference components reflect different concepts (Legendre, 2014) then the replacement components cannot reflect the same concept in the alternative methods. They argued, among others, that the replacement component of the BAS framework (e.g. $Repl_{WB}$) is the only true measure of species replacement because it is independent of absolute richness difference ($Rich_{WB}$). As a response to this study, Podani and Schmera (2016) questioned the assumption that any replacement component should be independent from relative richness difference. They showed that even the absolute (raw) replacement ($Repl_{WB}$) and richness difference ($Rich_{WB}$) components are not independent and thus concluded that independence of a raw richness difference measure should not be a criterion that any replacement measures should satisfy. Consequently, there is still no consensus on the interpretation and meaning of the replacement components of the BAS and POD frameworks.

As a contribution to this debate, we introduced here the SET framework that separates beta diversity into nestedness-related (I) and nestedness-unrelated (RC) components by partitioning the Weiher-Boylen diversity, as well as the Jaccard and Sørensen dissimilarities (Suppl. Table 2). Following the argumentation of Baselga and Leprieur (2015), it is easy to see that if the same index is partitioned into nestedness-related and nestedness-unrelated components, and the nestedness-related components are properly formulated, then the nestedness-unrelated components should reflect the same concept. More specifically, neither the replacement component of the BAS framework conceptualizes replacement (i.e. it cannot be used as a measure of Replacement PPC), nor the nestedness-unrelated component of the SET framework conceptualizes replacement (i.e. it should be called a measure of Replacement PPC). To facilitate understanding the different forms, first we identify components of beta diversity that reflect the existence of single $PPCs$, or the simultaneous existence of two or three $PPCs$.

4.2. Properties of beta diversity components

We examined the components of eight beta diversity partitions, belonging to three families and three frameworks (Suppl. Table 2). Considering the studies of Jost et al. (2011) and Legendre and de Cáceres (2013), we describe five properties (abbreviated as PRO 1 to PRO 5) and examine which components possess them.

PRO 1 – Minimum. The component has zero effect only if it is not part of beta diversity.

PRO 2 – Maximum. The component equals to total beta diversity only if the component is exclusive contributor of beta diversity.

PRO 3 – Raw measure. The component is regarded as a raw measure if the contribution of pattern to beta diversity is expressed in terms of the number of species.

PRO 4 – Relativized to total species richness. The component is

regarded as one relativized to total species richness if the contribution of pattern to beta diversity is expressed as the percentage of the number of species present in the two sites combined.

PRO 5 – Relativized to average species richness. The component is regarded as one relativized to average species richness if the contribution of pattern to beta diversity is expressed as the percentage of the average number of species present in the two sites under study.

According to our interpretation, PRO 1 and PRO 2 are essential in characterizing any beta diversity components. This is because if a component possesses PRO 1, then we can be sure that zero value indicates the absence of the phenomenon to be indicated. Similarly, if a component possesses PRO 2, then we can be sure that the maximum value of the component indicates the exclusive presence of the phenomenon to be indicated. PROs 3, 4 and 5 have only interpretative value: PRO3 shows whether a particular component is expressed in terms of the number of species, as a percentage of the total species richness of the site pair (PRO 4, for example "Jaccard standardization"), or the percentage of the average species richness of the site pair (PRO 5, for example "Sørensen standardization"). We examine the performance of the measures in different community patterns using analytical approaches in the next section.

4.3. Results

We found that almost all replacement components possess PROs 1 and 2; they were zero when the Replacement PPC was absent from the given pattern and indicated their maximum value when beta diversity contained only the Replacement PPC (Suppl. Table 3). The exceptions were $Repl_{BJ}$ and $Repl_{BS}$ (Suppl. Table 3). These components violated the maximum property when an anti-nested pattern was studied: both showed that the Replacement PPC was the exclusive component of beta diversity even when the Richness difference PPC also appeared in the pattern. Nestedness-related components (Suppl. Table 4) and richness difference components (Suppl. Table 5) satisfied the requirements PRO 1 & 2.

We also observed that the Weiher-Boylen diversity and its components (POD Framework: $Repl_{WB}$ and $Rich_{WB}$; SET framework: I_{WB} & RC_{WB}) can always be interpreted as raw measures (PRO 3; Suppl. Tables 3–5): they express the number of species forming $PPCs$ and derived concepts. Similarly, the Jaccard dissimilarity and its components derived from the POD ($Repl_J$ and $Rich_J$) and SET (I_J & RC_J) frameworks can always be interpreted as relativized measures expressed as percentage of the number of species in both sites (PRO 4; Suppl. Tables 3–4). Finally, the Sørensen dissimilarity and its components derived from the POD ($Repl_S$ and $Rich_S$) and SET (I_S & RC_S) frameworks can always be interpreted as relativized measures expressed as percentage of the average number of species in both sites (PRO 5; Suppl. Tables 3–5). In contrast, components of the BAS framework did not always possess PRO3, PRO4 or PRO5. This is because the different components are not uniformly relativized (see also Schmera and Podani, 2011).

5. Analysis of an actual data set

To demonstrate the practical utility of our approach, we analysed data from fish assemblages of Death Valley, USA (Smith, 1978), in which the number of sites (i.e., drainage units) was 5 and the number of species was 8. The file was downloaded from the example folder of Atmar and Patterson (1995). The Death Valley fish community shows high beta diversity with limited amount of community overlap. Smith (1978) explained this pattern by the isolation of the study sites from one another as well as by frequent extinction events in the past.

Each pair of sites was examined to identify (1) which $PPCs$ contribute to beta diversity and (2) whether the intersection of nestedness and beta diversity exists (Fig. 3). We found that in most of the cases, beta diversity was formed by Richness difference and Replacement $PPCs$ (for 8 of the 10 site pairs), whereas in one case by Richness

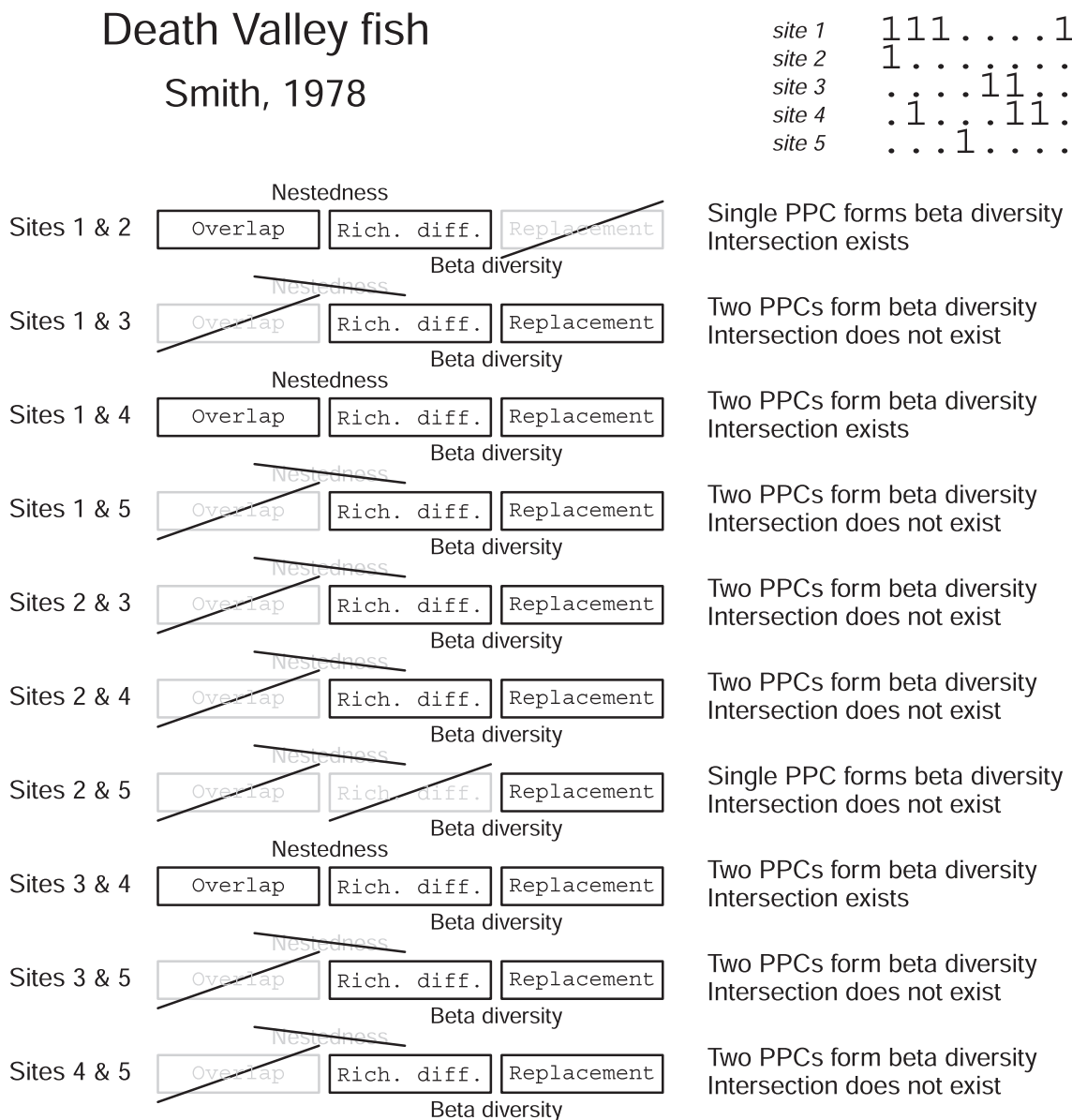


Fig. 3. Assessing the existence of pairwise pattern components (PPCs) as well as two ecological concepts (i.e. nestedness and beta diversity) in site pairs of the Death Valley fish community data (Smith, 1978). The top-right corner contains the data matrix. 1 denotes presence while 0 s are replaced by dots to denote absences. Sites are in rows while species in columns.

difference PPC only (sites 1 & 2) and in another case by Replacement PPC only (sites 2 & 5). These results demonstrate that Richness difference and Replacement PPCs can form beta diversity, individually or together.

We examined also whether the intersection of nestedness and beta diversity exists (Fig. 3). Obviously, Richness difference PPC represents their intersection. If the Richness difference PPC does not exist (e.g. sites 2 & 5), then nestedness and beta diversity have no intersection. However, due to the complexity of nestedness (Podani and Schmera, 2012; Feoli et al., 2019), the existence of Richness difference PPC does not necessarily predict that the intersection of nestedness and beta diversity exists. Although the Richness difference PPC is present in 9 pairs of sites, it forms the intersection of nestedness and beta diversity in only 3 cases (Fig. 3: site pairs 1 & 2, 1 & 4, and 3 & 4). In the remaining 6 cases, nestedness does not exist, because the Overlap PPC does not exist (Fig. 3: site pairs 1 & 3, 1 & 5, 2 & 3, 2 & 4, 3 & 5, and 4 & 5).

Let us examine the behaviour of the measures (indicators) belonging to different frameworks. Site pair 1 & 3 contains Richness difference

and Replacement PPCs, while the Overlap PPC is absent (Fig. 3). This pattern is called an anti-nested pattern. That is, beta diversity is formed by Richness difference and Replacement PPCs. In agreement with this, $\beta_{WB} = 6$ (6 species form Richness difference and Replacement PPCs, Table 3). The POD framework states that beta diversity (β_{WB}) can be divided into replacement ($Repl_{WB} = 4$) and richness difference components ($Rich_{WB} = 2$), while according to the SET framework, division is possible into a relative complement of nestedness in beta diversity ($RC_{WB} = 6$, i.e. 6 of the 6 species form that part of beta diversity, which is unrelated to nestedness) and an intersection of nestedness and the beta diversity component ($I_{WB} = 0$, i.e. none of the species forming beta diversity is related to nestedness). The interpretation of the Jaccard and Sørensen families is similarly straightforward, but raw measures are standardized by the number of species (Jaccard: 6 species) or presences (Sørensen: 6 presences) occurring in the site pair. The BAS framework in contrast states that replacement is the only component (Jaccard family: $Repl_{BJ}$, Sørensen family: $Repl_{BS}$) of beta diversity (i.e. $J = Repl_{BJ}$ and $S = Repl_{BS}$). This is obviously not true because both Richness

Table 3
Comparison of the three beta partitioning frameworks (BAS, POD and SET) using site pairs 1 & 3 (A) and 1 & 4 (B) from the data set of Death Valley fish assemblages (Smith, 1978). The presence-absence matrix is provided in Fig. 3, while the formulas of components are found in Supplementary Table 2.

Index	BAS framework			POD framework			SET framework		
	Family (abbreviation)	Value	Component name (abbreviation)	Value	Component name (abbreviation)	Value	Component name (abbreviation)	Value	Value
(A) Site pair 1 & 3									
Weiher-Boyley (β_{WB})	6	NOT AVAILABLE			Replacement ($Repl_{WB}$)	4	Relative complement of nestedness in beta diversity (RC_{WB})	6	
		NOT AVAILABLE			Richness difference ($Rich_{WB}$)	2	Intersection of nestedness and beta diversity (I_{WB})	0	
	6/6	Replacement ($Repl_{WB}$)		4/4	Richness difference ($Rich_{WB}$)	4/6	Relative complement of nestedness in beta diversity (RC_{WB})	6/6	
Jaccard (J)			Nestedness resultant component (Nes_{JL})	0	Richness difference ($Rich_{JL}$)	2/6	Intersection of nestedness and beta diversity (I_L)	0/6	
Sørensen (S)	6/6	Replacement ($Repl_{JL}$)		2/2	Richness difference ($Rich_{JL}$)	4/6	Relative complement of nestedness in beta diversity (RC_{JL})	6/6	
		Nestedness resultant component (Nes_{JL})		0	Richness difference ($Rich_{JL}$)	2/6	Intersection of nestedness and beta diversity (I_L)	0/6	
(B) Site pair 1 & 4									
Weiher-Boyley (β_{WB})	5	NOT AVAILABLE			Replacement ($Repl_{WB}$)	4	Relative complement of nestedness in beta diversity (RC_{WB})	4	
		NOT AVAILABLE			Richness difference ($Rich_{WB}$)	1	Intersection of nestedness and beta diversity (I_{WB})	1	
	5/6	Replacement ($Repl_{WB}$)		4/5	Richness difference ($Rich_{WB}$)	4/6	Relative complement of nestedness in beta diversity (RC_{WB})	4/6	
Jaccard (J)			Nestedness resultant component (Nes_{JL})	5/6-4/5	Richness difference ($Rich_{JL}$)	1/6	Intersection of nestedness and beta diversity (I_L)	1/6	
Sørensen (S)	5/7	Replacement ($Repl_{JL}$)		2/3	Richness difference ($Rich_{JL}$)	4/7	Relative complement of nestedness in beta diversity (RC_{JL})	4/7	
		Nestedness resultant component (Nes_{JL})		5/7-2/3	Richness difference ($Rich_{JL}$)	1/7	Intersection of nestedness and beta diversity (I_L)	1/7	

difference and Replacement PPCs are present (Fig. 3). Consequently, the replacement components of the BAS framework (i.e. $Repl_{BJ}$ and $Repl_{BS}$) are not adequate indicators of the ecological concept of replacement (manifested by the Replacement PPC).

Site pair 1 & 4 contains Overlap, Richness differences and Replacement PPCs (Fig. 3). Nestedness exists and is formed by Overlap and Richness difference PPCs. Beta diversity also exists and is formed by Richness difference and Replacement PPCs. In agreement with this, $\beta_{WB} = 5$ (5 species form Richness difference and Replacement PPCs, Table 3). The POD framework states that beta diversity (β_{WB}) can be divided into replacement ($Repl_{WB} = 4$) and richness difference components ($Rich_{WB} = 1$). The SET framework states that beta diversity (β_{WB}) can be divided into a relative complement of nestedness in beta diversity ($RC_{WB} = 4$, i.e. 4 of the 5 species form that part of beta diversity, which is unrelated to nestedness) and an intersection of nestedness and the beta diversity component ($I_{WB} = 1$, i.e. 1 of the 5 species form that part of beta diversity which is related to nestedness). As above, raw measures are standardized by the number of species (Jaccard index: 6 species) or presences (Sørensen index: 7 presences) occurring in the site pair. No interpretation can be connected to PPCs in the BAS framework.

6. Discussion

Extracting meaningful information from community data is a highly challenging task of community ecology. As beta diversity components are receiving increasing attention in this mission, here we focused on what these components reveal from presence-absence community data. To do this job in a transparent way, we considered the components of beta diversity as indicators, whereas the ecological concepts or phenomena intended to be reflected was the indicandum. Using algebraic assessments, we examined whether indicators reflect exclusively a given indicandum. We found that when a community pattern is anti-nested, the BAS framework falsely indicates a 100% share of replacement. These suggest that beta diversity components do not necessarily reflect the assumed ecological concept and therefore we argue that ecological indicators should always be selected carefully.

In order to extract information from community data, we suggest that conceptual distinction be made among *community patterns* (the objects on which inference should be made), *pairwise pattern components* (PPCs, building blocks of community patterns that reflect unique responses of communities and thus represent the phenomena to be indicated) and *measures* (which quantify a relevant property of PPCs and derived concepts). This distinction allows researchers to clearly separate the studied objects (community patterns), the community phenomena reflecting the effects of processes (PPCs and derived ecological concepts), and the indicators of these phenomena (measures). The key concept suggested here is the *pairwise pattern component*, which allows ecologists to infer whether the process shaping community differentiation has no effect (indicated by Overlap), or whether it changes composition (Replacement) or richness (Richness difference). Obviously, this suggestion does not link the observed pattern to a well-defined underlying process, but similarly to the approach of Vellend (2010), it allows the mechanisms to be classified through the effect on the community pattern. In this respect, the application of PPCs is a significant step in extracting information from community patterns.

Pioneers of community ecology inferred the existence of structuring forces from the community patterns observed (Clements, 1916; Gleason, 1926). These so-called idealized community patterns have received increasing attention recently (Leibold and Mikkelsen, 2002; Presley et al., 2010; Schmera et al., 2018). Here we suggest a functional classification of these idealized community patterns for the first time based on PPCs. Our classification suggests that idealized community patterns were attractive because each of them presents a unique combination of the response types of communities (no effect, change in species identities or in richness). We also examined how beta diversity

components indicate the corresponding ecological concept in some of these idealized community patterns.

We have demonstrated that indices suggested by Podani and Schmera (2011, 2016), Carvalho et al. (2013) and Legendre (2014) are the indicators of ecological concepts formulated by PPCs in any presence-absence-based community pattern occurring in nature. In this respect, PPCs present the theoretical background of these measures. However, the picture is less clear and ecological interpretation becomes difficult for the abundance-based analogues of these indices (Baselga, 2010, 2012; Podani et al., 2013; Legendre, 2014). Further studies are needed to examine the possibility if a similar framework of PPCs can be developed for abundance data.

To fulfil the increasing need for quantifying how nestedness contributes to beta diversity, we proposed a new partitioning of beta diversity based on set theory (SET framework), and compared the performance of the existing partitions of beta diversity (i.e. BAS, POD and SET frameworks) in light of the PPCs. We found that, for anti-nested patterns (and for every pair of sites where Replacement and Richness Difference PPCs are present and Overlap PPC is absent), the replacement components of the BAS partitioning framework ($Repl_{BJ}$ and $Repl_{BS}$) indicate the exclusive presence of Replacement PPC even when Richness difference PPC is also present. This means that these components are not adequate measures of the Replacement PPC, or these measures of the BAS framework are not compatible with PPCs.

In his original proposal, Baselga (2010) suggested the partition of the Sørensen dissimilarity (Sørensen, 1948) into replacement (Simpson dissimilarity) and nestedness-resultant components (Suppl. Table 2). The Simpson index (Simpson, 1943) has always been regarded as a classical dissimilarity measure that is insensitive to the richness difference of the two communities studied (Lennon et al., 2001; Koleff et al., 2003; Carvalho et al., 2013). In agreement with this, the rationale for selecting the Simpson formula was “to describe spatial turnover [i.e. replacement] without the influence of richness gradients” (Baselga, 2010, p. 136). Based on this information, the Simpson dissimilarity seemed to be an ideal choice. Unfortunately, richness-insensitivity remains also when the two sites do not share any species (anti-nested pattern). In this case, beta diversity (Sørensen dissimilarity) equals the measure of species replacement (Simpson dissimilarity) and indicates incorrectly that beta diversity consists only of the Replacement PPC (see also Carvalho et al., 2013). Consequently, Simpson's dissimilarity indicates replacement but does not do it exclusively in relation to the Sørensen dissimilarity. This non-exclusive detection (Suppl. Table 3) explains that, in our view, Simpson dissimilarity as linked to the Sørensen dissimilarity cannot be used as an indicator of replacement or, if it is used anyway, then the analysis of anti-nested patterns should be avoided. A similar conclusion can be drawn about the replacement component of the BAS framework developed in the Jaccard family.

The most important problem with the BAS partitioning framework is that it does not define the replacement phenomenon (Replacement PPC) and its raw measure. Consequently, there is no clear link between the phenomenon (Replacement PPC) that one can intuitively see as species number instead of some proportion, and the measure (replacement component of beta diversity). In contrast, the POD and the SET frameworks apply raw measures (those belonging to the Weiher-Boyle family, Suppl. Table 3) and thus allow us to link the phenomena (e.g. replacement, richness difference, nestedness-related component of beta diversity, and nestedness-unrelated component of beta diversity) to the corresponding measures ($Repl_{WB}$, $Rich_{WB}$, I_{WB} , and RC_{WB}).

Another problem with the BAS framework is related to the scaling (or relativization or commensurability) of beta diversity and its components. As this issue has provoked a discussion already (Baselga, 2012; Baselga and Leprieur, 2015; Carvalho et al., 2013; Podani and Schmera, 2016; Schmera and Podani, 2011), we do not repeat the arguments here; we only highlight that the insensitivity of the Simpson dissimilarity to richness difference is caused by both the numerator and the denominator of the index. That is, if we assume that the numerator

quantifies the raw measure, then scaling should also add some properties to the measure. As the BAS framework defines no raw measure and because beta diversity and its components are differently scaled (Suppl. Table 2), the formulation of the framework with an intuitively expected behavior (each measure detects exclusively the corresponding phenomenon) is rather challenging. Our analysis of anti-nested pattern clearly shows that the replacement components of the BAS framework ($Repl_{BJ}$ and $Repl_{BS}$) indicate 100% Replacement PPC in beta diversity and thus implies the absence of Richness difference PPC incorrectly.

Recently, Baselga and Leprieur (2015) have argued that the replacement component of the BAS framework (e.g. $Repl_{BJ}$) is the only true measure of species replacement because it is independent of absolute richness difference ($Rich_{WB}$). As a response to this study, Podani and Schmera (2016) questioned the assumption that any replacement component should be independent of relative richness difference. They also showed that even the absolute (raw) replacement ($Repl_{WB}$) and richness difference ($Rich_{WB}$) components are not independent and thus concluded that the independence of a raw richness difference measure cannot be a criterion that replacement measures should satisfy. Our present results show that the replacement components of the BAS framework ($Repl_{BJ}$ and $Repl_{BS}$) can quantify not only the Replacement PPC but also the Richness difference PPC. Based on these results, we argue that the replacement components of the BAS framework cannot be regarded as true measures of Replacement PPC. It seems that the price of its richness independence, a criterion that is not an essential property of a replacement measure (Podani and Schmera, 2016), is that these measures do not measure the Replacement PPC exclusively.

According to our present knowledge, beta diversity can be partitioned in three different ways into: 1) replacement and nestedness-related components (BAS framework), 2) replacement and richness difference components (POD framework) and 3) nestedness-related and nestedness-unrelated components (SET framework). Following the logic of Baselga and Leprieur (2015), the successful integration of different partitioning frameworks into ecological theory requires that the terminology (e.g. replacement component) accurately reflects the concept to be expressed (e.g. the phenomenon of replacement). Our results based on algebraic evidence show that the replacement components of the BAS framework do not exclusively quantify the Replacement PPC, while the replacement and richness difference components of the POD framework are exclusive measures of Replacement and Richness difference PPCs, respectively. Consequently, the replacement component of the POD framework correctly quantifies the Replacement PPC. Moreover, our algebraic results combined with logical considerations suggest that richness difference is the natural complement of replacement as implied by the POD framework. The other side of the coin is that beta diversity can be partitioned into nestedness-related and nestedness-unrelated components. Our findings on some basic properties of the components demonstrate that although the nestedness-related components of the BAS framework could be properly formulated, their complements cannot be defined as replacement as suggested by the BAS framework. In sum, beta diversity can be partitioned into replacement and richness difference components (as suggested by the POD framework), or into nestedness-related and nestedness unrelated components (as suggested by the SET framework). However, the combination of the two partitioning schemes does not work because nestedness-related components are not the complements of replacement in forming beta diversity.

We are by no means stating that the Simpson dissimilarity (Simpson, 1943) is an inadequate measure of Replacement PPC. On the contrary, we agree with Baselga and Leprieur (2015) that large-scale patterns of species replacement after having controlled for species richness difference have fundamental importance in biogeographic studies (Harrison et al., 1992; Leprieur and Oikonomou, 2014). Even more, we can imagine an infinite variety of species replacement measures (Appendix 2 in Podani and Schmera, 2016). Our algebraic results clearly indicate that linking the Simpson dissimilarity to the Sørensen dissimilarity with

the assumption that the Simpson index measures the replacement component of the Sørensen index is not necessarily valid.

Until now, we focused only on the analytical aspect of inference from community patterns. In some cases, however, field sampling of communities is challenging, and the sampling procedure might result in a biased presence-absence matrix. The most likely bias is that species are not detected even if they are present in the study sites. Such unobserved species might cause that the observed Richness difference *PPC* is in reality a Replacement or even an Overlap *PPC*, and thus our analytical conclusions would be flawed. To avoid such sampling bias, special attention should be paid to the representativeness of samples (see Cao et al., 2002; Ramsey and Hewitt, 2005).

In this paper, we extended the mathematical toolkit of numerical ecology with a new beta diversity partitioning framework (SET framework). We suggested the application of pairwise pattern components (*PPCs*) to support inference on communities. Using algebraic approaches, we examined the performance of the existing (BAS and POD) and new (SET) frameworks in detecting *PPCs* (Overlap, Replacement and Richness difference). We found that the replacement components of the BAS framework might indicate exclusively the Replacement *PPC* when the Richness difference *PPC* is also present. Consequently, if the objective of the study is to indicate an ecological phenomenon, then the replacement component of the BAS framework cannot be recommended, unless the anti-nested patterns are disregarded. For a correct inference, we suggest the application of the replacement and the richness difference components of the POD framework, or the nestedness-related and the nestedness-unrelated components of the SET framework depending on whether nestedness should be considered.

CRediT authorship contribution statement

Dénes Schmera: Conceptualization, Funding acquisition, Investigation, Methodology, Visualization, Writing - original draft, Writing - review & editing. **János Podani:** Conceptualization, Investigation, Methodology, Writing - review & editing. **Pierre Legendre:** Conceptualization, Investigation, Methodology, Writing - review & editing.

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.

Acknowledgements

This work was supported the GINOP (Gazdaságfejlesztési és Innovációs Operatív Program, Hungary) 2.3.3-15-2016-00019 and NKFI (Nemzeti Kutatási, Fejlesztési és Innovációs Hivatal, Hungary) K128496 grants.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106540>.

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