



## A new look at functional beta diversity

Carlo Ricotta<sup>a,b,\*</sup>, Sandrine Pavoine<sup>c,2</sup>

<sup>a</sup> Department of Environmental Biology, University of Rome 'La Sapienza', Rome, Italy

<sup>b</sup> National Biodiversity Future Centre (NBFC), Palermo, Italy

<sup>c</sup> Centre d'Ecologie et des Sciences de la Conservation (CESCO), Muséum National d'Histoire Naturelle, CNRS, Sorbonne Université, 75005 Paris, France

### ARTICLE INFO

#### Keywords:

Algorithmic dissimilarity of Kosman and Gregorius  
Beta diversity decomposition  
Functional dissimilarity  
Functional resemblance  
Taxonomic similarity  
Ternary diagram

### ABSTRACT

The variability in species composition among a set of sampling sites, or beta diversity, is considered a key signature of the ecological processes that shape the spatial structure of species assemblages. In this paper, we propose to decompose this variability into three additive components: i) the standard similarity in the (relative) abundances of species among sites, ii) the degree of functional *dissimilarity* between individuals of distinct species among sites, and iii) the degree of functional *similarity* between individuals of distinct species among sites, or beta redundancy. These three components can be used to portray the functional resemblance among sites on a ternary diagram. With the resulting ternary diagram of 'functional resemblance' we can relate various aspects of taxonomic and functional variability among sites to community assembly processes more completely than just looking at individual components. The potential of this method is shown with real data on the functional turnover of Alpine species along a primary succession on glacial deposits in northern Italy.

### 1. Introduction

The amount of variation in species composition among sites, or beta diversity, is considered a fundamental tool for exploring the ecological processes that shape the spatial structure of species assemblages. Since the seminal work of Whittaker (1972), many different methods and measures have been proposed for summarizing beta diversity (Lande, 1996; Koleff et al., 2003; Anderson, 2006; Jost, 2007; Tuomisto, 2010a, 2010b; Anderson et al., 2011; Chao and Chiu, 2016; Legendre and De Cáceres, 2013; Ricotta, 2017; Chao and Ricotta, 2019). One of the most commonly used consists in computing beta diversity as the mean compositional dissimilarity between pairs of sampling units (i.e., relevés, quadrats, assemblages, etc. which we will now generally refer to as plots). The general idea behind this approach is that for a set of plots, compositional heterogeneity or beta diversity increases with increasing mean dissimilarity (i.e., dispersion) between plots (Whittaker, 1972; Izsak and Price, 2001; Koleff et al., 2003; Chao and Chiu, 2016).

To compute dissimilarity-based beta diversity, standard measures, such as the Jaccard or the Bray-Curtis coefficients (Legendre and Legendre, 2012) were originally used. Such measures quantify taxonomic (i.e., species) differences between plots based only on species presences

and absences or on abundance data, thus assuming that all species are equally and maximally distinct from each other, while neglecting information on functional differences among species. In the last decades however, several 'functional dissimilarity measures' have been proposed (reviewed in Lengyel and Botta-Dukát, 2023). Such measures take into account information on functional differences among species. Therefore, they are expected to improve correlation between community data and ecosystem functioning, as the species traits directly or indirectly influence these processes (Mouchet et al., 2010; Mason and de Bello, 2013).

A neglected outcome of the idea that distinct species possess varying degrees of functional dissimilarity (discussed by Ricotta et al., 2023 in the context of within-site diversity) is that the ecological information associated to the functional resemblance structure among plots is much richer and complex than that obtained from standard taxonomic dissimilarity measures. Note that in this paper, the term resemblance is used *sensu* Orloci (1972) as a generic concept referring to "any type of distances, dissimilarities, similarities, correlation, association or proximity measures among the study objects" (Podani and Schmera, 2021).

Assuming that all species are equally and maximally distinct, standard similarity/dissimilarity measures in the range [0,1] are complementary to each other. For example, given two plots  $h$  and  $k$  with species

\* Corresponding author at: Department of Environmental Biology, University of Rome 'La Sapienza', Rome, Italy.

E-mail address: [carlo.ricotta@uniroma1.it](mailto:carlo.ricotta@uniroma1.it) (C. Ricotta).

<sup>1</sup> ORCID: <https://orcid.org/0000-0003-0818-3959>.

<sup>2</sup> ORCID: <https://orcid.org/0000-0003-2767-6484>.

relative abundances  $p_{jh}$  and  $p_{jk}$  ( $j = 1, 2, \dots, N$ ), where  $N$  is the number of species with non-zero abundance in at least one of the two plots, the well-known [Bray and Curtis \(1957\)](#) dissimilarity and similarity coefficients  $D_{BC}$  and  $S_{BC}$  can be expressed as  $D_{BC} = \frac{\sum_{j=1}^N |p_{jh} - p_{jk}|}{\sum_{j=1}^N (p_{jh} + p_{jk})}$  and  $S_{BC} = 1 - D_{BC} = \frac{2 \times \sum_{j=1}^N \min\{p_{jh}, p_{jk}\}}{\sum_{j=1}^N (p_{jh} + p_{jk})}$ , respectively, such that  $S_{BC} + D_{BC} = 1$ . Hence, looking only at one of them is enough to capture the entire information on the resemblance structure of both plots (the reason for using relative abundances instead of absolute abundances for the calculation of  $D_{BC}$  and  $S_{BC}$  will be clear in the following sections). This is however not the case for functional resemblance, where the distinct species contribute to varying degrees to the similarity/dissimilarity structure among plots. In this latter case, it seems natural to decompose standard (abundance-based) taxonomic dissimilarity into two complementary functional components: the extent of functional *dissimilarity* among individuals of the species that differ between the two plots, and the extent of functional *similarity* among individuals of the species that differ between the two plots. For dissimilarity measures in the range [0,1] these two components, together with the standard taxonomic similarity between individuals of the *same* species in both plots, can be used to display the functional resemblance structure between plots on a ternary diagram.

An essential requirement to appropriately decompose functional resemblance is that, for a given pair of plots, functional dissimilarity is always lower than standard compositional dissimilarity. However, many of the existing measures of functional dissimilarity do not fulfill this requirement ([Ricotta et al., 2020](#)). In this paper, we will first introduce the proposed additive decomposition of functional beta diversity, together with its basic requirements. Next, the potential of this approach for a more comprehensive analysis of the amount of functional variation among sites is shown with a worked example on the functional turnover of Alpine species along a primary succession in northern Italy.

## 2. A step by step introduction to beta diversity decomposition

Let  $d_{ij}$  be a measure of functional dissimilarity between species  $i$  and  $j$  ( $i, j = 1, 2, \dots, N$ ) in the range [0,1] and  $s_{ij}$  be the corresponding functional similarity  $s_{ij} = 1 - d_{ij}$ . The functional dissimilarities  $d_{ij}$  summarize uni- or multivariate differences in the trait values between species such that  $d_{ij} = d_{ji}$  and  $d_{ii} = 0$ . For two plots  $h$  and  $k$ , let  $D_F$  be a measure of functional dissimilarity ( $0 \leq D_F \leq 1$ ) that is computed by taking into account the actual functional differences  $d_{ij}$  between the species in both plots. Examples of such measures can be found e.g., in [Rao \(1982\)](#), [Chao et al. \(2014\)](#), [Pavoine and Ricotta \(2014\)](#), [Ricotta et al., \(2020, Appendix S1\)](#), [Ricotta et al., \(2021a\)](#) and in the worked example of this paper.

Further, let  $D_S$  be a corresponding measure of taxonomic dissimilarity between  $h$  and  $k$  ( $0 \leq D_S \leq 1$ ) that is computed solely from the differences in species abundances between both plots (i.e. assuming that all species are maximally dissimilar from each other, such that  $d_{ij} = 1$  for all  $i \neq j$ ). If  $D_S \geq D_F$ , which is an intuitively reasonable condition given the definition of  $D_F$  and  $D_S$ , we can decompose the resemblance structure between  $h$  and  $k$  into three additive components that describe distinct facets of the taxonomic and functional differences between both plots. For instance, the complements of  $D_F$  and  $D_S$ :

$$S_F = 1 - D_F \quad (1a)$$

and

$$S_S = 1 - D_S \quad (1b)$$

summarize the functional similarity  $S_F$  and the corresponding taxonomic (i.e., species) similarity  $S_S$  ( $S_S \leq S_F$ ) between the plots  $h$  and  $k$ , respectively. Like for  $D_F$  and  $D_S$ ,  $S_F$  is computed by taking into account the actual functional (dis)similarities between the species in both plots, whilst  $S_S$  is computed solely from the differences in species abundances

between plots assuming that  $s_{ij} = 0$  ( $d_{ij} = 1$ ) for all species  $i \neq j$ .

The third component of the proposed beta diversity decomposition is the difference between  $D_S$  and  $D_F$  (i.e., the excess of taxonomic dissimilarity between  $h$  and  $k$  over functional dissimilarity):

$$R_\beta = D_S - D_F = S_F - S_S \quad (2)$$

$R_\beta$  represents the extent of functional *similarity* between individuals of the species unshared by the plots. From an ecological viewpoint,  $R_\beta$  can be interpreted as the degree to which individuals of species unshared by the plots support the same ecological functions. Therefore, [Ricotta et al. \(2020, 2021a\)](#) termed this quantity beta redundancy.

According to Eq. (2), taxonomic dissimilarity between plots  $D_S$  can be thus additively decomposed into two distinct functional fractions: the degree of functional *dissimilarity* between individuals of distinct species  $D_F$  and the corresponding degree of functional *similarity* between individuals of distinct species, or beta redundancy  $R_\beta$  such that  $D_S = D_F + R_\beta$ . Hence, the overall functional resemblance structure among pairs of plots can be decomposed into three additive components,  $D_F$ ,  $R_\beta$ , and  $S_S$  each with its own ecological meaning.

A relevant aspect of this decomposition is that for  $d_{ij}$  in the range [0,1] the pairwise functional dissimilarity  $D_F$ , beta redundancy  $R_\beta$ , and taxonomic similarity  $S_S$  sum up to one:

$$D_F + R_\beta + S_S = 1 \quad (3)$$

This offers the opportunity to use a ternary diagram to represent the functional resemblance structure among plots in graphical form. A ternary diagram displays the values of three variables  $a$ ,  $b$ , and  $c$  as point coordinates on an equilateral triangle. The values of the variables must sum to a fixed constant, usually 1 (or 100 %), such that  $a = 1 - (b + c)$ . The corners of the triangle represent a scenario in which one variable has a value of one and the other two variables have a value of zero. The values of each variable progressively decrease with increasing distance from the related corner ([Ricotta et al., 2023](#)). For example, if a point falls close to the  $D_F$  corner, this means that the corresponding pair of plots shows high functional dissimilarity, whereas closeness to the opposite side of the triangle reflects high functional similarity. Likewise, if a point falls close to the  $R_\beta$  corner, the corresponding pair of plots shows high beta redundancy; if the point falls close to the opposite side of this corner, the plots show low beta redundancy.

With this ‘ternary diagram of functional resemblance’ we can thus graphically represent the compositional structure of a given set of plots in terms of pairwise functional dissimilarity, beta redundancy and taxonomic similarity. Therefore, ternary diagrams can be used to explore the ecological processes that shape different facets of the amount of variation in species composition among plots more exhaustively than by looking only at differences in functional dissimilarity ([Podani and Schmera, 2011](#); [Ricotta et al., 2023](#)).

## 3. Worked example

### 3.1. Data

To illustrate the behavior of the proposed approach, we used the same data of [Ricotta et al. \(2021a, 2021b\)](#). The dataset is composed of a community composition matrix of 45 species in 59 plots of approximately 25 m<sup>2</sup> sampled by [Caccianiga et al. \(2006\)](#) along a primary succession at the foreland of the Rutor Glacier (Northern Italy). The abundance of each species was assessed with a five-point ordinal scale transformed to ranks.

Based on the age of the glacial deposits, the plots were originally grouped by [Caccianiga et al. \(2006\)](#) into three successional stages. However, [Ricotta et al. \(2021a, 2021b\)](#) showed that in terms of functional beta diversity, the last two stages of the chronosequence are not significantly different from each other. Therefore, in this paper we classified all plots in the community composition matrix into two

distinct groups: early successional plots (17 plots) and late successional plots (42 plots).

For all species, six key traits were used, which are related to the species global spectrum of form and function (Díaz et al., 2016): canopy height (CH; mm), leaf dry mass content (LDMC; %), leaf dry weight (LDW; mg), specific leaf area (SLA;  $\text{mm}^2 \times \text{mg}^{-1}$ ), leaf nitrogen content (LNC; %), and leaf carbon content (LCC; %). Data on species abundances and functional traits are available in Ricotta et al., (2016, Appendix S2), and Caccianiga et al., (2006, Table 2), respectively, and in the `adiv` (R package) object ‘RutorGlacier’ (Pavoine, 2020). Note that in this paper, we assume that the same species in different plots have the same trait values. However, the proposed approach is not necessarily based on this assumption and can be easily extended to account for intraspecific trait variability. All R scripts used in this study are available in the electronic [Supplementary Material](#) to this paper.

### 3.2. Methods

As in Ricotta et al. (2021a, 2021b), the trait values were first standardized to zero mean and unit standard deviation. Then, we used the Euclidean distance to compute a matrix of pairwise functional distances between the 45 species from the standardized functional traits. The functional distances were next rescaled in the unit range by dividing each distance by the maximum value in the distance matrix. For all pair of plots in both successional stages, we finally used the algorithmic dissimilarity coefficient of Kosman (1996) and Gregorius et al. (2003)  $D_{KG}$  to calculate the three components of functional resemblance: functional dissimilarity, beta redundancy and taxonomic similarity.

A necessary condition to additively decompose functional resemblance is that, for two plots  $h$  and  $k$ , functional dissimilarity  $D_F$  is always lower than taxonomic dissimilarity  $D_S$ . This prevents negative redundancy values, which would obviously be meaningless. However, as shown by Ricotta et al., (2020, Appendix S1), none of the existing analytical measures of functional dissimilarity conforms to this ‘redundancy property’.

In contrast to standard analytical measures of functional dissimilarity, the algorithmic dissimilarity  $D_{KG}$  conforms to the redundancy property (proof in Ricotta et al., 2021a, Appendix S1). The measure, which has been originally developed to measure genetic differences between populations, is based on the best possible match between the species in  $h$  and  $k$  in order to minimize the total functional differences between the plots. For two plots  $h$  and  $k$ , with  $n$  individuals in both plots, each individual in  $h$  is matched to an individual in  $k$  with the goal of minimizing the sum of functional differences between the individuals in both plots. The  $n$  pairs are formed such that all individuals in each plot are used only once. The functional dissimilarity  $D_{KG}$  is then obtained as the mean dissimilarity between each pair of matched individuals (Kosman and Leonard, 2007). However, since the actual number of individuals in  $h$  and  $k$  is usually not the same, to get a complete association between the individuals in both plots, the matching procedure is performed on the species relative abundances  $p_{jh}$  and  $p_{jk}$  in  $h$  and  $k$ , respectively.

Mathematically, the functional dissimilarity  $D_{KG}$  between plots  $h$  and  $k$  can be formulated as (Gregorius et al., 2003):

$$D_{KG} = \min_{\pi} \sum_{i=1}^N \sum_{j=1}^N \pi(i,j) \times d_{ij} \quad (4)$$

where  $\pi(i,j)$  is the relative abundance of species  $i$  in plot  $h$  that is matched with species  $j$  in plot  $k$ .

The use of species relative abundances  $p_{jh}$  (with  $0 \leq p_{jh} \leq 1$  and  $\sum_{j=1}^N p_{jh} = 1$ ) for the calculation of functional dissimilarity is justified by the observation that in most cases, ecologists are interested in exploring how the fraction of individuals that support a given ecological function differ between two plots (i.e. how the functional traits are proportionally

distributed among the species in both plots), irrespective of the species absolute abundances in each plot.

Finding the optimal association between the species abundances in  $h$  and  $k$  is a special kind of linear optimization problem (Dantzig and Thapa, 1997). Since  $D_{KG}$  is essentially a mean dissimilarity between pairs of individuals, if the functional dissimilarity  $d_{ij}$  ranges from 0 (minimal dissimilarity between matched individuals) to 1 (maximal dissimilarity between matched individuals),  $D_{KG}$  also ranges from 0 to 1. Similarly, the complement of functional dissimilarity  $D_{KG}$  represents a measure of pairwise functional similarity  $S_{KG} = 1 - D_{KG}$  between  $h$  and  $k$  that can be calculated as the optimal matching between the species abundances in  $h$  and  $k$  so as to maximize the mean similarity  $s_{ij} = 1 - d_{ij}$  between the species in both plots.

Kosman (2014) further showed that if all species in  $h$  and  $k$  are maximally dissimilar from each other (i.e. if  $d_{ij} = 1$  for all species  $i \neq j$ ), functional dissimilarity  $D_{KG}$  reduces to the classical Bray-Curtis dissimilarity computed from the species relative abundances  $p_{jk}$ :

$$D_{BC} = \sum_{j=1}^N |p_{jh} - p_{jk}| / \sum_{j=1}^N (p_{jh} + p_{jk}) = \frac{1}{2} \sum_{j=1}^N |p_{jh} - p_{jk}| \quad (5)$$

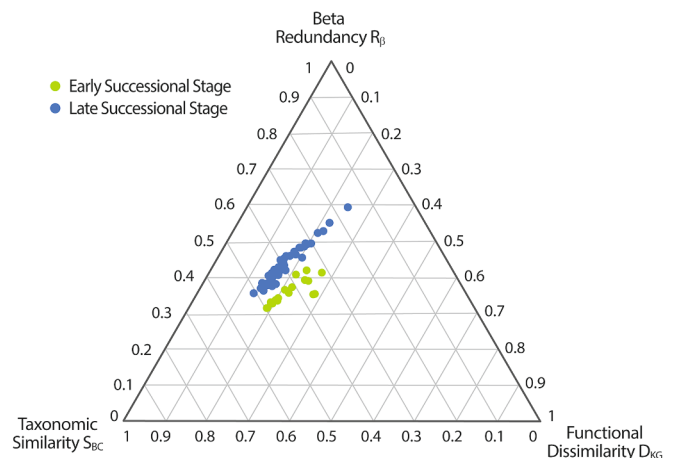
such that  $D_{KG} \leq D_{BC}$ . This allows to decompose functional similarity  $S_{KG}$  into standard taxonomic similarity between the individuals of the same species in both plots

$$S_{BC} = 1 - D_{BC} = \sum_{j=1}^N \min\{p_{jh}, p_{jk}\} \quad (6)$$

and the degree of functional similarity between the individuals of distinct species in both plots, or beta redundancy  $R_{\beta} = D_{BC} - D_{KG} = S_{KG} - S_{BC}$  such that  $D_{KG} + R_{\beta} + S_{BC} = 1$  (see Eq. (3)). An R function for the calculation of  $D_{BC}$ ,  $D_{KG}$  and  $R_{\beta}$  can be found in the R package `adiv` (Pavoine, 2020).

To test for differences in the beta diversity of both successional stages using all three components of the functional resemblance structure, we calculated the mean values of functional dissimilarity  $\bar{D}_{KG}$ , beta redundancy  $\bar{R}_{\beta}$ , and taxonomic similarity  $\bar{S}_{BC}$  of each plot from all other plots of the same successional stage (see Ricotta et al., 2021b). The resulting values were then plotted on the ternary diagram of Fig. 1 with the R package `adegraphics` (Siberchicot et al., 2017).

Once the mean values  $\bar{D}_{KG}$ ,  $\bar{R}_{\beta}$ , and  $\bar{S}_{BC}$  of the two groups of plots have been plotted on the ternary diagram, testing for differences in



**Fig. 1.** Ternary diagram of functional resemblance for the early and late successional plots of Alpine vegetation on glacial deposits in northern Italy. The results of db-MANOVA show that the two successional stages significantly differ in their overall functional resemblance structure at  $p < 0.001$  ( $F = 10.23$ , Bray-Curtis dissimilarity and 10,000 randomizations).

functional resemblance between the two successional stages of the Alpine vegetation essentially reduces to testing whether the distribution of the two groups of plots on the ternary diagram does not overlap. Therefore, we tested for differences in the ternary composition of both groups of plots with distance-based multivariate analysis of variance (db-MANOVA; Anderson, 2001) and the Bray-Curtis dissimilarity with the R package PERMANOVA (Vicente-Gonzalez and Vicente-Villardón, 2021).

db-MANOVA is a multivariate extension of standard analysis of variance which uses any multivariate dissimilarity measure of choice to test for differences between two or more distinct groups of plots. The purpose of db-MANOVA is to contrast the within-group dissimilarities among plots with their between-group dissimilarities. The greater the between-group dissimilarities in comparison to the within-group dissimilarities, the more likely the groups of plots differ in their ternary composition (Anderson, 2001). First, based on the actual  $\bar{D}_{KG}$ ,  $\bar{R}_\beta$  and  $\bar{S}_{BC}$  values of each plot, the within-group and between-group dissimilarities among plots were calculated with the Bray-Curtis dissimilarity, and a multivariate analogue of Fisher's F-ratio was calculated directly from the dissimilarity matrix. A P-value was next calculated using 10,000 permutations in which the single plots were randomly reassigned to the two successional stages while maintaining the three-dimensional vector of the functional resemblance values  $\bar{D}_{KG}$ ,  $\bar{R}_\beta$  and  $\bar{S}_{BC}$  of each plot unchanged (Anderson, 2006; Ricotta et al., 2021b).

At least for exploratory data analysis, Ricotta et al. (2023) considered this procedure appropriate for handling compositional data with a constant sum constraint. Those looking for statistical methods explicitly developed for the analysis of compositional data can refer to Aitchison (1986) or Van den Boogaart and Tolosana-Delgado (2013).

Finally, for each single resemblance measure,  $\bar{D}_{KG}$ ,  $\bar{R}_\beta$  and  $\bar{S}_{BC}$ , we separately tested for differences between the two successional stages with standard univariate ANOVA and 10,000 permutations of individual observations between both groups of plots. Since db-MANOVA does not identify which particular resemblance measure is significantly different between groups of plots, the analysis of variance of the single components  $\bar{D}_{KG}$ ,  $\bar{R}_\beta$  and  $\bar{S}_{BC}$  can then be used as a kind of post-hoc test to explore differences between multiple groups using each component at a time.

#### 4. Results

Ternary diagrams have been first used for the analysis of beta diversity/dissimilarity by Podani and Schmera (2011). Such diagrams allow us to visualize the relative fractions of three variables on a two-dimensional graph. Aside from visual inspection, the point patterns in a ternary diagram can also be analyzed statistically. According to db-MANOVA, the successional stages in the ternary diagram of Fig. 1 significantly differ in their overall functional resemblance structure ( $F = 10.23$ ,  $p < 0.001$ ). As shown in Table 1, the random dispersal

**Table 1**

Mean (SD) values of average functional dissimilarity  $\bar{D}_{KG}$ , beta redundancy  $\bar{R}_\beta$  and taxonomic (i.e., species) similarity  $\bar{S}_{BC}$  of each plot from all other plots of the same successional stage. Pairwise comparisons of index differences between both successional stages were performed with standard univariate ANOVA. P-values were obtained by randomly permuting individual plots between the successional stages (10,000 permutations). \*\*\* = significant at  $p < 0.001$ ; NS = not significant at  $p < 0.05$ .

	Early successional plots (17 plots)	Late successional plots (42 plots)
Functional dissimilarity $\bar{D}_{KG}$ ***	0.217 (0.033)	0.165 (0.024)
Beta redundancy $\bar{R}_\beta$ ***	0.370 (0.030)	0.440 (0.050)
Taxonomic similarity $\bar{S}_{BC}$ NS	0.413 (0.054)	0.395 (0.072)

mechanisms that drive the colonization of the glacial deposits in the early successional stages give rise to significantly higher values of mean functional dissimilarity between plots  $\bar{D}_{KG}$ , and to lower values of functional redundancy among individuals of different species  $\bar{R}_\beta$ . By contrast, while the taxonomic (i.e., species) turnover among plots  $\bar{S}_{BC}$  is approximately the same in both successional stages, in the late successional stages the species in one plot tend to be replaced by functionally similar species in the other plots, thus leading to an increased level of functional beta redundancy among different sampling units (Caccianiga et al., 2006).

#### 5. Discussion

The aim of this paper was to bring together distinct aspects of the analysis of functional beta diversity, redundancy, and community similarity into a coherent system. Some of these results were previously discussed in the context of within-site diversity, or alpha diversity (e.g., Ricotta et al., 2023) but can easily be extended to beta diversity. Resemblance measures that can be partitioned into complementary components are extremely valuable since the resultant elements can be related to a variety of distinct ecological processes that determine the structure of species assemblages (Baselga, 2010; Podani and Schmera, 2011; Podani et al., 2013; Ricotta et al., 2023). In this context, the relevant questions are: how to decompose the pairwise functional resemblance between plots, how to graphically represent this decomposition and how to test for significant differences in functional resemblance among groups of plots.

Unlike standard similarity/dissimilarity coefficients which possess a simple binary structure, the increased complexity of functional resemblance arises from the relaxation of the constraint that all species are equally and maximally distinct. If species exhibit varying degrees of functional dissimilarity, two plots with no species in common can either be functionally identical or entirely functionally distinct depending on the degree of functional dissimilarity  $d_{ij}$  between the species in both plots. Accordingly, looking only at differences in functional dissimilarity between plots provides just a partial view of their taxonomic and functional variability.

The concept of beta redundancy has been first introduced by Ricotta et al. (2020) as the amount of taxonomic dissimilarity between two plots not expressed by functional dissimilarity. Ricotta et al. (2020) used a relative measure of beta redundancy  $R_\beta^* = (D_S - D_F)/D_S$ . By contrast, due to the additive nature of the proposed dissimilarity decomposition, in this paper we used the absolute difference  $R_\beta = D_S - D_F$ . Redundancy is maximal for two functionally identical plots ( $D_F = 0$ ) with no species in common ( $D_S = 1$ ). On the other hand, redundancy is zero when the species turnover between two plots is associated to a complete functional turnover such that  $D_S = D_F$  and hence  $R_\beta = 0$ .

Beta redundancy tells us to what degree the species that differ between two plots are able to perform the same ecological functions: the higher the value of beta redundancy, the lower the association between species turnover and functional turnover. Accordingly, beta redundancy might be related to chief ecological processes, such as species dispersal, habitat filtering, or competitive exclusion. For instance, one might assume that the lower functional dissimilarity and the higher beta redundancy observed in the late successional plots of our worked example could be attributed to the role of local species interactions (biotic filters), which impose more intense constraints on plant species recruitment compared to the abiotic filters present in the early successional stages (Klanderud, 2010; Meineri et al., 2020).

From a more 'technical' viewpoint, in order to get a valid measure of beta redundancy, the functional dissimilarity  $D_F$  should always be lower than the corresponding taxonomic dissimilarity  $D_S$ . Surprisingly, Ricotta et al. (2020) showed that many of the existing indices of functional dissimilarity do not conform to this 'redundancy property'. Therefore, they cannot be used to appropriately decompose functional resemblance



into non-negative additive fractions. In this view, the transition from a species-based ecology to a trait-based ecology has important implications not only in biological terms (Díaz and Cabido, 2001), but also in statistical terms.

To address this issue, Ricotta et al. (2020) introduced a tree-based measure of functional dissimilarity that conforms to the redundancy property. However, being based on a hierarchical representation which is the more natural way for describing the evolutionary relationships among species, the functional dissimilarity coefficient of Ricotta et al. (2020) is more adequate to represent the phylogenetic dissimilarity among plots rather than their functional differences. Ricotta et al. (2021a) thus suggested to summarize functional dissimilarity with the algorithmic coefficient of Kosman and Gregorius which does not depend on a tree-based species organization. While  $D_{RG}$  allows for appropriately calculating functional dissimilarity, we hope that this is just the first in a series of new measures. Indeed, the search for a new class of functional dissimilarity measures appears to be a very promising research direction, aiming to enrich the ecologist's toolbox with new, more up-to-date instruments for exploring various aspects of functional resemblance and their ecological drivers.

### Funding information

The research was funded by the European Union – *NextGenerationEU* within the National Biodiversity Future Center.

### CRedit authorship contribution statement

**Carlo Ricotta:** Writing – original draft, Methodology, Formal analysis, Conceptualization. **Sandrine Pavoine:** Writing – review & editing, Software, Methodology, Formal analysis.

### 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.

### Data availability

All data are already in the public domain

### Acknowledgments

We thank Evsey Kosman and an anonymous reviewer for their insightful comments on a previous version of this paper.

### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2024.112136>.

### References

- Aitchison, J., 1986. *The Statistical Analysis of Compositional Data*. Chapman and Hall, London.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Anderson, M.J., 2006. Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62, 245–253.
- Anderson, M.J., Crist, T.O., Chase, J.M., Vellend, M., Inouye, B.D., Freestone, A.L., Sanders, N.J., Cornell, H.V., Comita, L.S., Davies, K.F., Harrison, S.P., Kraft, N.J.B., Stegen, J.C., Swenson, N.G., 2011. Navigating the multiple meanings of beta diversity: a road map for the practicing ecologist. *Ecol. Lett.* 14, 19–28.
- Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* 19, 134–143.
- Bray, J.R., Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecol. Monogr.* 27, 325–349.
- Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M., Cerabolini, B.E.L., 2006. The functional basis of a primary succession resolved by CSR classification. *Oikos* 112, 10–20.
- Chao, A., Chiu, C.H., Jost, L., 2016. Bridging the variance and diversity decomposition approaches to beta diversity via similarity and differentiation measures. *Methods Ecol. Evol.* 7, 919–928.
- Chao, A., Chiu, C.H., Jost, L., 2014. Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annu. Rev. Ecol. Evol. Syst.* 45, 297–324.
- Chao, A., Ricotta, C., 2019. Quantifying evenness and linking it to diversity, beta diversity, and similarity. *Ecology* 100, e02852.
- Dantzig, G.B., Thapa, M.N., 1997. *Linear Programming*. Springer, New York.
- Díaz, S., Cabido, M., 2001. Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655.
- Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth, C., Colin Prentice, I., Garnier, E., Bönsch, G., Westoby, M., Poorter, H., Reich, P.B., Moles, A.T., Dickie, J., Gillison, A.N., Zanne, A.E., Gorné, L. D., 2016. The global spectrum of plant form and function. *Nature* 529, 167–171.
- Gregorius, H.R., Gillet, E.M., Ziehe, M., 2003. Measuring differences of trait distributions between populations. *Biom. J.* 45, 959–973.
- Izsak, C., Price, R.G., 2001. Measuring  $\beta$ -diversity using a taxonomic similarity index, and its relation to spatial scale. *Mar. Ecol. Prog. Ser.* 215, 69–77.
- Jost, L., 2007. Partitioning diversity into independent alpha and beta components. *Ecology* 88, 2427–2439.
- Klanderud, K., 2010. Species recruitment in alpine plant communities: the role of species interactions and productivity. *J. Ecol.* 98, 1128–1133.
- Koleff, P., Gaston, K.J., Lennon, J.J., 2003. Measuring beta diversity for presence-absence data. *J. Anim. Ecol.* 72, 367–382.
- Kosman, E., 1996. Difference and diversity of plant pathogen populations: A new approach for measuring. *Phytopathology* 86, 1152–1155.
- Kosman, E., 2014. Measuring diversity: From individuals to populations. *Eur. J. Plant Pathol.* 138, 467–486.
- Kosman, E., Leonard, K.J., 2007. Conceptual analysis of methods applied to assessment of diversity within and distance between populations with asexual or mixed mode of reproduction. *New Phytol.* 174, 683–696.
- Lande, R., 1996. Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* 76, 5–13.
- Legendre, P., De Cáceres, M., 2013. Beta diversity as the variance of community data: dissimilarity coefficients and partitioning. *Ecol. Lett.* 16, 951–963.
- Legendre, P., Legendre, L., 2012. *Numerical Ecology*. Elsevier, Amsterdam.
- Lengyel, A., Botta-Dukát, Z., 2023. A guide to between-community functional dissimilarity measures. *Ecography* 11, e06718.
- Mason, N.W.H., de Bello, F., 2013. Functional diversity: A tool for answering challenging ecological questions. *J. Veg. Sci.* 24, 777–780.
- Meineri, E., Klanderud, K., Guittar, J., Goldberg, D.E., Vandvik, V., 2020. Functional traits, not productivity, predict alpine plant community openness to seedling recruitment under climatic warming. *Oikos* 129, 13–23.
- Mouchet, M.A., Villéger, S., Mason, N.W.H., Moullot, D., 2010. Functional diversity measures: an overview of their redundancy and their ability to discriminate community assembly rules. *Funct. Ecol.* 24, 867–876.
- Orlaci, L., 1972. On objective functions of phytosociological resemblance. *Am. Midl. Nat.* 88, 28–55.
- Pavoine, S., 2020. *adiv*: An R package to analyse biodiversity in ecology. *Methods Ecol. Evol.* 11, 1106–1112.
- Pavoine, S., Ricotta, C., 2014. Functional and phylogenetic similarity among communities. *Methods Ecol. Evol.* 5, 666–675.
- Podani, J., Ricotta, C., Schmera, D., 2013. A general framework for analyzing beta diversity, nestedness and related community-level phenomena based on abundance data. *Ecol. Complex.* 15, 52–61.
- Podani, J., Schmera, D., 2011. A new conceptual and methodological framework for exploring and explaining pattern in presence-absence data. *Oikos* 120, 1625–1638.
- Podani, J., Schmera, D., 2021. Generalizing resemblance coefficients to accommodate incomplete data. *Eco. Inform.* 66, 101473.
- Rao, C.R., 1982. Diversity and dissimilarity coefficients: A unified approach. *Theor. Popul. Biol.* 21, 24–43.
- Ricotta, C., 2017. Of beta diversity, variance, evenness, and dissimilarity. *Ecol. Evol.* 7, 4835–4843.
- Ricotta, C., de Bello, F., Moretti, M., Caccianiga, M., Cerabolini, B.E.L., Pavoine, S., 2016. Measuring the functional redundancy of biological communities: A quantitative guide. *Methods Ecol. Evol.* 7, 1386–1395.
- Ricotta, C., Laroche, F., Szeidl, L., Pavoine, S., 2020. From alpha to beta functional and phylogenetic redundancy. *Methods Ecol. Evol.* 11, 487–493.
- Ricotta, C., Kosman, E., Laroche, F., Pavoine, S., 2021a. Beta redundancy for functional ecology. *Methods Ecol. Evol.* 12, 1062–1069.
- Ricotta, C., Kosman, E., Caccianiga, M., Cerabolini, B.E.L., Pavoine, S., 2021b. On two dissimilarity-based measures of functional beta diversity. *Eco. Inform.* 66, 101458.
- Ricotta, C., Podani, J., Schmera, D., Bacaro, G., Maccherini, S., Pavoine, S., 2023. The ternary diagram of functional diversity. *Methods Ecol. Evol.* 14, 1168–1174.
- Siberchicot, A., Julien-Laferrrière, A., Dufour, A.B., Thioulouse, J., Dray, S., 2017. *adegraphics*: An S4 lattice-based package for the representation of multivariate data. *The R Journal*. 9, 198–212. <https://journal.r-project.org/archive/2017/RJ-2017-042/index.html>.
- Tuomisto, H., 2010a. A diversity of beta diversities: straightening up a concept gone awry. Part 1. Defining beta diversity as a function of alpha and gamma diversity. *Ecography* 33, 2–22.

Tuomisto, H., 2010b. A diversity of beta diversities: straightening up a concept gone awry. Part 2. Quantifying beta diversity and related phenomena. *Ecography* 33, 23–45.

Van den Boogaart, K.G., Tolosana-Delgado, R., 2013. *Analyzing Compositional Data with R*. Springer, Heidelberg.

Vicente-Gonzalez, L., Vicente-Villardón, J.L., 2021. PERMANOVA: multivariate analysis of variance based on distances and permutations. R Package Version (2). <https://CRAN.R-project.org/package=PERMANOVA>.

Whittaker, R., 1972. Evolution and measurement of species diversity. *Taxon* 21, 213–251.

**R scripts** used for the worked example of the functional beta diversity decomposition proposed in the main text. The scripts were written with R version 4.3.2.

**Disclaimer:** users of this code are cautioned that, while due care has been taken and it is believed accurate, its use and results are solely the responsibilities of the user.

```
# Package loading:

install.packages("adiv")
install.packages("adegraphics")
install.packages("PERMANOVA")

library(adiv) # version 2.2
library(adegraphics) # version 1.0-21
library("PERMANOVA") # version 0.2.0

# Data loading:

data(RutorGlacier)

# Functional dissimilarities between species:

fundis <- dist(scale(RutorGlacier$Traits2[1:6]))
fundis <- fundis/max(fundis)

# Relative abundance of species in plots:

prop <- sweep(RutorGlacier$Abund, 1, rowSums(RutorGlacier$Abund), "/")

# vector that indicates which plot belongs to which group (either early or
late successional stage). Plots are in the same order as in table named
prop above.

groups <- RutorGlacier$Fac
groups[groups == "mid"] <- "late"

# Data analyses:

propsplitted <- split(prop, as.factor(groups))
prop_Early <- propsplitted[[1]]
prop_Late <- propsplitted[[2]]

frameDKG_Early<- betaUniqueness(prop_Early, fundis)
frameDKG_Late <- betaUniqueness(prop_Late, fundis)

D_KG_Early<- frameDKG_Early$DKG # Pairwise functional dissimilarities
between plots of early successional stage.
S_BC_Early<- 1-frameDKG_Early$DR # Pairwise species similarity between
plots of early successional stage.
R_beta_Early <- frameDKG_Early $DR- frameDKG_Early$DKG # Pairwise beta
redundancy between plots of early successional stage.

D_KG_Late <- frameDKG_Late$DKG # Pairwise functional dissimilarities
between plots of late successional stage.
S_BC_Late<- 1-frameDKG_Late$DR # Pairwise species similarity between plots
of late successional stage.
R_beta_Late <- frameDKG_Late $DR- frameDKG_Late$DKG # Pairwise beta
redundancy between plots of late successional stage.
```

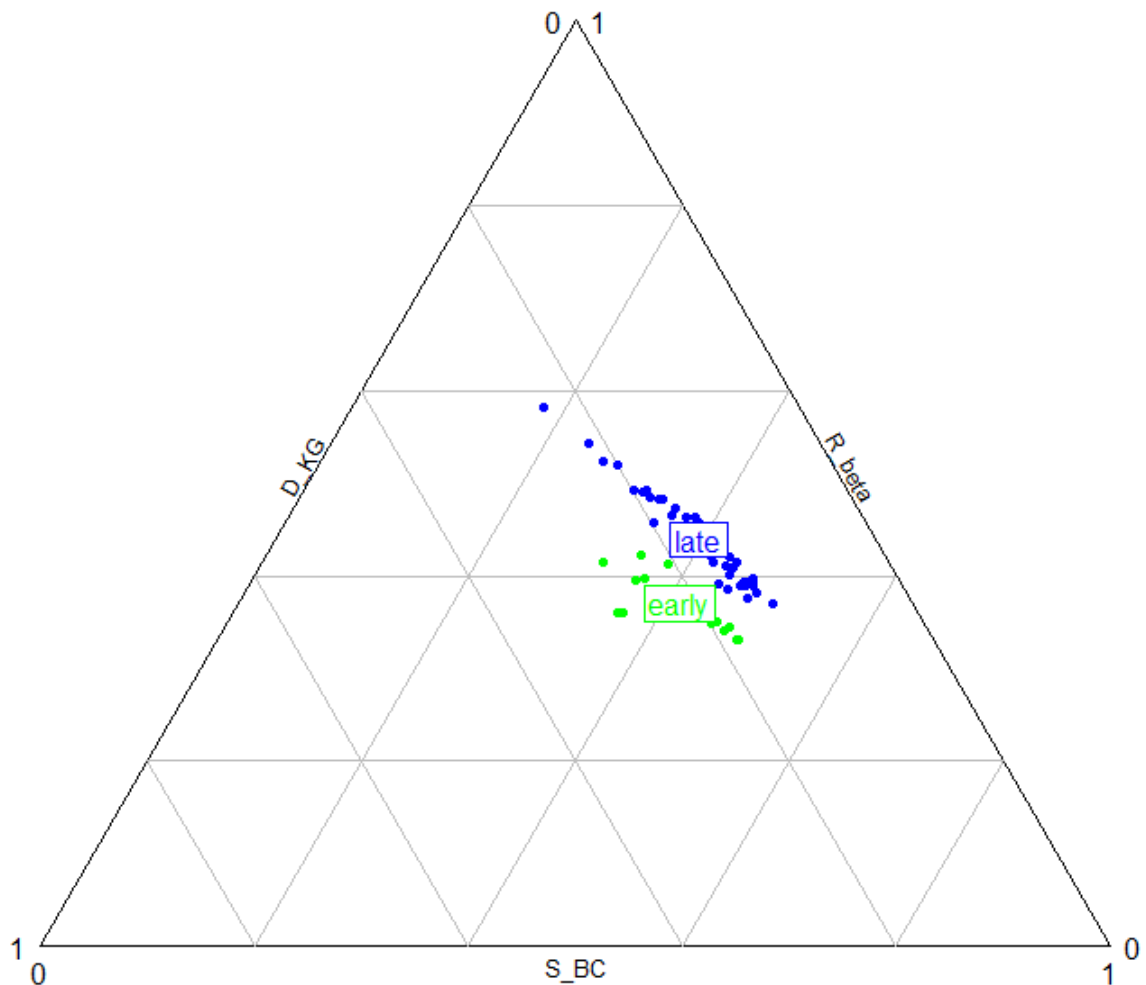
```
# Below are calculated the average functional dissimilarities, beta
redundancy and species similarity of each plot from the other plots of the
same group. Plots are in the same order as in vector named "groups" and
table named "prop".
```

```
D_KG_bar_Early <- sapply(1:17, function(i) mean(D_KG_Early[i, -i]))
S_BC_bar_Early<- sapply(1:17, function(i) mean(S_BC_Early[i, -i]))
R_beta_bar_Early <- sapply(1:17, function(i) mean(R_beta_Early[i, -i]))
D_KG_bar_Late <- sapply(1:42, function(i) mean(D_KG_Late[i, -i]))
S_BC_bar_Late<- sapply(1:42, function(i) mean(S_BC_Late[i, -i]))
R_beta_bar_Late <- sapply(1:42, function(i) mean(R_beta_Late[i, -i]))
```

```
# Graphical display for an equivalent of Figure 1 of main text
```

```
TAB_Early <- cbind.data.frame(D_KG_bar_Early, S_BC_bar_Early,
R_beta_bar_Early)
TAB_Late <- cbind.data.frame(D_KG_bar_Late, S_BC_bar_Late, R_beta_bar_Late)
names(TAB_Early) <- names(TAB_Late) <- c("D_KG", "S_BC", "R_beta")
TAB <- rbind.data.frame(TAB_Early, TAB_Late)
```

```
triangle.class(TAB, as.factor(groups), starSize = 0, ellipseSize=0,
adjust=FALSE, showposition =FALSE, col=c("green", "blue"))
```





```

# Pairwise comparisons of index differences between both successional
stages (Table 1 of main text)

# 1. Functional dissimilarity

mean(D_KG_bar_Early)
# [1] 0.2171854

sd(D_KG_bar_Early)
# [1] 0.03259282

mean(D_KG_bar_Late)
# [1] 0.164982

sd(D_KG_bar_Late)
# [1] 0.02423698

# 2. Beta redundancy

mean(R_beta_bar_Early)
# [1] 0.3701257

sd(R_beta_bar_Early)
# [1] 0.02989589

mean(R_beta_bar_Late)
# [1] 0.4396643

sd(R_beta_bar_Late)
# [1] 0.04991988

# 3. Species (dis)similarity

mean(S_BC_bar_Early)
# [1] 0.412689
sd(S_BC_bar_Early)
# [1] 0.0541672

mean(S_BC_bar_Late)
# [1] 0.3953538

sd(S_BC_bar_Late)
# [1] 0.07227821

# 4. Global PERMANOVA test

TAB4Ptest <- DistContinuous(TAB, , "Bray_Curtis")

Ptest <- PERMANOVA(TAB4Ptest, as.factor(groups), nperm=10000)

Ptest
##### PERMANOVA Analysis #####
# MANOVA
#      Explained  Residual df Num df Denom      F-exp    p-value p-value adj.
# Total 0.047524   0.26475    1     57 10.23187 0.00089991 0.0008999

```