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Beta redundancy for functional ecology

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Abstract

1. Functional beta redundancy has been recently defined as the fraction of species dissimilarity between two plots not expressed by functional dissimilarity. As such, it summarizes to what degree the compositional differences between two plots mirror their functional differences.
2. A fundamental condition to obtain an appropriate measure of functional beta redundancy is that the functional dissimilarity between the plots is always lower (or at least not higher) than the corresponding species dissimilarity. However, many of the extant measures of functional dissimilarity do not fulfil this requirement.
3. To overcome this problem, a class of tree-based indices of functional dissimilarity that conform to the above 'redundancy property' has been recently proposed. However, functional dissimilarity measures need not necessarily be based on a hierarchical representation of the species functional relationships.
4. In this paper, we introduce an algorithmic index of functional dissimilarity that conforms to the redundancy property. Since it does not rely on a hierarchical species organization, the proposed index allows to calculate functional beta redundancy in a more suitable way to the non-hierarchical structure of the species functional relationships. The behaviour of the proposed measure is illustrated with data on the species functional turnover along real and simulated ecological gradients.

KEYWORDS
algorithmic measure, functional dissimilarity, local versus global scaling, redundancy property, standardized versus non-standardized coefficients

1 | INTRODUCTION

In a recent paper, Ricotta et al. (2020) introduced the notion of beta redundancy to quantify the fraction of species dissimilarity between two plots not expressed by functional or phylogenetic dissimilarity. Therefore, beta redundancy basically summarizes to what degree the species turnover between two plots is associated with a functional or phylogenetic turnover. This might help to infer the processes underpinning diversity distribution in space and time.

For a pair of plots P and Q, the chief condition to get a meaningful index of beta redundancy is that the functional or phylogenetic dissimilarity D_F is always lower than the corresponding species dissimilarity D_S. However, many of the most popular indices of functional and phylogenetic dissimilarity violate this condition, thus leading to the paradoxical situation of a negative beta redundancy (see Ricotta et al., 2020; Appendix S1). To overcome this problem, Ricotta et al. (2020) proposed a class of tree-based indices of functional and phylogenetic dissimilarity between plots that conform to the condition $D_F \leq D_S$. The indices are said 'tree-based' because they depend on a functional or phylogenetic tree with species as tips and branches that express functional or phylogenetic relationships between species. However, while phylogenies have a hierarchical, non-overlapping structure, functional diversity tends to have a non-hierarchical, overlapping structure (Von Euler & Svensson, 2001). Therefore, being based on a hierarchical structure of species relationships, the proposed tree-based measures are the more natural way for summarizing plot-to-plot phylogenetic dissimilarity, whereas a tree-based representation of the species functional relationships is not unanimously accepted by ecologists (see e.g. Pavoine, 2016; Poos et al., 2009). For example, Maire et al. (2015) and Loiseau et al. (2017) have reported that dendrograms tend to overestimate the functional distance between species leading to a biased assessment of functional relatedness.

The aim of this paper is thus to propose an abundance-based version of the algorithmic index of functional dissimilarity developed by Kosman (1996) and Gregorius et al. (2003) that conforms to the requirement $D_F \le D_S$. Since it does not rely on a tree-based species organization, the proposed measure allows to calculate functional beta redundancy in a way that is more appropriate to the non-hierarchical structure of functional relationships among species. Two worked examples with artificial and actual datasets, both representing the species functional turnover along ecological gradients are used to illustrate our approach.

2 | AN ALGORITHMIC MEASURE OF FUNCTIONAL BETA REDUNDANCY

Let P and Q be two plots with species relative abundance vectors $P = (p_1, \ldots, p_i, \ldots, p_S)$ and $Q = (q_1, \ldots, q_i, \ldots, q_S)$, where $0 \le p_i \le 1$, $\sum_{i=1}^{S} p_i = 1$ (similarly, $0 \le q_i \le 1$, $\sum_{i=1}^{S} q_i = 1$) and S is the total number of species in both plots. The information on the species functional organization within both plots is usually represented by a symmetric $S \times S$ matrix of pairwise functional dissimilarities d_{ij} between species i and j with $0 \le d_{ij} \le 1$, $d_{ij} = d_{ji}$ and $d_{ii} = 0$ ($i,j = 1, 2, \ldots S$). Also, let D_F be the functional dissimilarity between P and Q and D_S be the corresponding species dissimilarity. D_F is typically calculated by combining the species relative abundances in both plots with their functional dissimilarities d_{ij}, whereas D_S is calculated with the same species abundances as D_F but considering all species equally and maximally dissimilar from each other (i.e. with $d_{ij} = 1$ for all $i \ne j$).

The basic condition to obtain a meaningful and easily interpretable index of beta redundancy in the range $[0, 1]$ is that the functional dissimilarity D_F is lower (or at least not higher) than the corresponding species dissimilarity D_S. In this case, beta redundancy can be calculated as (Ricotta et al., 2020):

$$R_\beta = \frac{(D_S - D_F)}{D_S}, \tag{1}$$

while beta uniqueness, which is the complement of beta redundancy, can be calculated as:

$$U_\beta = 1 - R_\beta = \frac{D_F}{D_S}. \tag{2}$$

For $R_\beta = 0$, the species turnover between P and Q goes together with a corresponding functional turnover such that $D_F = D_S$. Hence, the compositional differences between P and Q mirror their functional differences. On the contrary, for $R_\beta = 1$, both plots are functionally identical to each other (i.e. $D_F = 0$). In this case, the species turnover between P and Q is not associated with a corresponding change in functional properties.

Kosman (1996) and Gregorius et al. (2003) independently proposed an algorithmic measure of (functional) dissimilarity which is based on the optimal overall matching between the species abundances in P and Q so as to minimize the mean functional dissimilarity between both plots. We can think of this operation as follows: for two plots of equal size P and Q with n individuals in each plot, to each individual in P an individual in Q is matched to obtain n pairs that minimize the sum of functional dissimilarities between individuals of the corresponding pairs (Kosman & Leonard, 2007). The pairs are constructed in such a way that all individuals in both plots are used only once. The dissimilarity between plots is then calculated by dividing this sum by n (the number of pairs of individuals). Finding the optimal matching between the species abundances in P and Q is known as the 'assignment problem' (Bellman et al., 1970), a special case of the transportation problem (TP) of linear programming (Hitchcock, 1941).

Note that, since the number of individuals in both plots is usually not the same, to get a complete matching between P and Q, this operation is best performed on the species relative abundances (see Gregorius et al., 2003). Note also that, since this index is a mean dissimilarity between matched pairs of individuals, if the functional dissimilarity between each pair of individuals is in the range $[0, 1]$, the resulting mean plot-to-plot dissimilarity also ranges between 0 and 1.

In terms of relative abundances, the algorithmic index of functional dissimilarity between plots P and Q can be defined as (Gregorius et al., 2003):

$$D_{KG} = \min_a \sum_{i=1}^{S} \sum_{j=1}^{S} d_{ij} \times a(i,j), \tag{3}$$

where $a(i, j)$ is the proportion of abundance of species i in plot P that is assigned to individuals of species j in plot Q. According to Kosman and Leonard (2007), if the functional dissimilarity between species is metric, then D_{KG} is also metric. Gregorius et al. (2003) and Kosman (2014) further showed that if all species are considered maximally dissimilar from each other (i.e. if $d_{ij} = 1$ for all species $i \ne j$ and $d_{ii} = 0$), D_{KG} will be equal to the Rogers (1972) dissimilarity:

$$D_R = \frac{1}{2} \sum_{i=1}^{S} |p_i - q_i|. \tag{4}$$

Otherwise, for any dissimilarity d_{ij} in the range $[0, 1]$, D_{KG} is always lower than D_R, thus conforming to the redundancy property that $D_F \le D_S$ (proof in Appendix S1). For those that are unfamiliar with the Rogers dissimilarity, it is worth mentioning that this coefficient is identical to the well-known Bray and Curtis (1957) dissimilarity (D_{BC}) computed on the species relative abundances: $D_{BC} = \sum_{i=1}^{S} |p_i - q_i| / \sum_{i=1}^{S} (p_i + q_i) = \sum_{i=1}^{S} |p_i - q_i| / 2$.

Accordingly, based on the algorithmic dissimilarity D_{KG}, we can define a measure of beta redundancy and uniqueness as:

$$R_\beta = \frac{\left(D_S - D_F\right)}{D_S} = \frac{\left(D_R - D_{KG}\right)}{D_R}, \tag{5}$$

and

$$U_\beta = \frac{D_F}{D_S} = \frac{D_{KG}}{D_R}, \tag{6}$$

where beta uniqueness is the fraction of species dissimilarity that is associated with functional dissimilarity, and beta redundancy is the fraction of species dissimilarity that is not associated with functional dissimilarity.

While the algorithmic dissimilarity of Kosman (1996) and Gregorius et al. (2003) has been originally developed in the field of genetics, in community ecology, a number of non-algorithmic measures based on minimum dissimilarity between the species in both plots have been proposed (Clarke et al., 2006; Clarke & Warwick, 1998; Izsak & Price, 2001; Ricotta & Burrascano, 2008; Ricotta, et al., 2016; Swenson, 2011). All these measures basically calculate the functional dissimilarity between a given species in the first plot and its closest functional relative in the second plot. This procedure is repeated for all species in P and Q and then averaged over both plots. The main difference is that D_{KG} is based on a (computationally intensive) optimal matching between the species abundances in both plots. This ensures that all individuals in P and Q are involved in the calculation of D_{KG}. By contrast, the 'suboptimal' matching performed by the non-algorithmic measures retains only nearest-neighbour differences between species for the calculation of functional dissimilarity. As a result, they generally underestimate functional dissimilarity compared to D_{KG}. For details, see Ricotta et al. (2020) (Appendix S2).

Beta uniqueness $U_\beta = D_F/D_S$ and redundancy $R_\beta = \left(D_S - D_F\right)/D_S$ are standardized coefficients that allow us to partition species dissimilarity into two complementary components: the degree of overlap between species dissimilarity and functional dissimilarity (U_β), and the fraction of species dissimilarity not expressed by functional dissimilarity (R_β) such that $U_\beta + R_\beta = 1$. However, these measures tell us nothing on the amount of similarity among plots. To get a more complete picture of the patterns of species and functional similarity among pairs of plots, non-standardized coefficients may be also used.

We start by noticing that if species dissimilarity D_S is bounded between zero and one, its complement $1 - D_S$ represents a suitable measure of species similarity among plots. At the same time, D_S can be also partitioned into two complementary components which represent the non-standardized versions of uniqueness and redundancy: functional dissimilarity D_F, and $D_S - D_F$ which is the (absolute) amount of species dissimilarity not expressed by functional dissimilarity. To differentiate $D_S - D_F$ from beta redundancy, in the remainder we will call this quantity 'dissimilarity gap' (Table 1 contains a summary of terms along with their definitions).

Therefore, for any functional dissimilarity coefficient that conforms to the redundancy property, we can define three non-standardized components: functional dissimilarity (D_F), dissimilarity gap ($D_S - D_F$) and species similarity ($1 - D_S$) such that $D_F + (D_S - D_F) + (1 - D_S) = 1$. For the algorithmic measures of Kosman (1996) and Gregorius et al. (2003), these three non-standardized components are D_{KG}, $D_R - D_{KG}$ and $1 - D_R$ respectively. Note, however, that the same approach can be used for any functional dissimilarity measure in the range [0, 1] that conforms to the redundancy property, including the tree-based functional and phylogenetic dissimilarity measures proposed by Ricotta et al. (2020).

TABLE 1 Summary of all redundancy components used in this study. All components are formulated in terms of species and/or functional dissimilarities

Component	Definitions and abbreviations
Functional dissimilarity	D_F
Species dissimilarity	D_S
Dissimilarity gap	$D_S - D_F$
Species similarity	$1 - D_S$
Functional similarity	$1 - D_F$
Beta uniqueness	$U_\beta = D_F/D_S$
Beta redundancy	$R_\beta = (D_S - D_F)/D_S$

3 | WORKED EXAMPLES

3.1 | Artificial data

The behaviour of the proposed measures was first evaluated on a small artificial dataset representing an ideal ecological gradient. The data consist of a matrix with the relative abundances of 15 species (S1–S15) in 10 plots (P1–P10). The matrix was built such that all species have unimodal abundance pattern of varying amplitude along the gradient (Table 1), while the corresponding functional dissimilarity matrix among species was built such that the interspecies dissimilarities reflect the species ecological differences along the simulated gradient (Appendix S2). To this end, the interspecies similarities were set proportional to the distance between the species optima (i.e. the locations along the gradient where the species show their maximum abundances).

To explore the response of the proposed measures to changes in species composition along the simulated gradient, we compared plot P1 with itself and with the remaining plots in terms of beta redundancy, species dissimilarity, functional dissimilarity and dissimilarity gap. All measures were calculated with a new R function available in Appendix S3 of this paper, which uses the same TP algorithm of Gregorius et al. (2003).

3.2 | Vegetation primary succession

We also explored the behaviour of the proposed measures on Alpine vegetation sampled by Caccianiga et al. (2006) along a primary succession. The dataset, which has been already used in previous papers on alpha and beta redundancy (Ricotta, de Bello, et al., 2016; Ricotta et al., 2020) is composed of 59 plots of approximately 25 m^2 sampled at the foreland of the Rutor Glacier (Northern Italy). For each plot, species abundances were measured with a 5-point ordinal scale transformed to ranks. Based on the age of the moraine deposits, the plots were then classified into three successional stages: early-successional stage (17 plots), mid-successional stage (32 plots) and late-successional stage (10 plots).

For all 45 plant species in the dataset, we selected six quantitative traits measured by Caccianiga et al. (2006) (Table 2), which provide a good representation of the 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; mm^2 × mg^{-1}), leaf nitrogen content (LNC; %) and leaf carbon content (LCC; %). All data are available in the data object named 'RutorGlacier' of the ADIV package (Pavoine, 2020) of R (R Core Team, 2021).

We used the Euclidean distance to calculate an interspecies dissimilarity matrix from the six functional traits. Before calculations, all traits were standardized to zero mean and unit standard deviation. The resulting functional distances among species were then rescaled to the unit range by dividing each distance by the maximum value in the distance matrix.

Based on the scaled matrix, we calculated the standardized and non-standardized functional dissimilarity components for all pairs of plots in each successional stage. We next used the PERMDISP test (Permutational Analysis of Multivariate Dispersions) of Anderson (2006) to test for differences in the dispersion of species dissimilarity D_R, functional dissimilarity D_{KG} and functional uniqueness U_β among the three successional stages.

4 | RESULTS

4.1 | Artificial data

The profile diagrams in Figure 1 (Podani & Miklós, 2002) show the response of species dissimilarity D_R, functional dissimilarity D_{KG}, beta redundancy R_β and dissimilarity gap $D_R - D_{KG}$ to changes in species composition along the artificial gradient in Table 1. The comparison of the first plot with itself and all other plots shows a monotonic increase of species and functional dissimilarity along the gradient. Note, however that, while for the pair of plots P1/P10, species dissimilarity reaches its maximum value (i.e. $D_R = 1$), meaning that P1 has no species in common with P10, functional dissimilarity does not reach its maximum value because the species in both plots are not completely functionally distinct. The profile diagrams in Figure 1 also show the main conceptual differences between standardized beta redundancy $R_\beta = \left(D_R - D_{KG}\right)/D_R$ and the non-standardized dissimilarity gap $D_R - D_{KG}$. In absolute terms, $D_R - D_{KG}$ increases along the first part of the gradient where the species turnover among plot P1 and the other plots is only weakly associated with a corresponding functional turnover. Then, it decreases along the second part of the gradient, where most of the species differences among P1 and the other plots are associated with functional differences among plots. By contrast, in relative terms, as species dissimilarity increases along the gradient, functional redundancy R_β tends to be progressively replaced by functional uniqueness $U_\beta = 1 - R_\beta$.

Note that for two identical plots, species dissimilarity D_S and functional dissimilarity D_F are both zero. In this case, beta uniqueness $U_{PP} = D_F/D_S$ and redundancy $R_{PP} = \left(D_S - D_F\right)/D_S$ are not defined. However, considering that beta uniqueness $U_\beta = D_F/D_S$ is a relative measure that relates plot-to-plot functional dissimilarity to its local maximum, we set by definition $U_{PP} = 0$ if $D_S = 0$.

TABLE 2 Artificial dataset with the relative abundances of 15 species (S1–S15) in 10 plots (P1–P10) ordered along an ideal ecological gradient. The matrix was built such that all species have unimodal response of varying amplitude and abundance to a hypothetical one-dimensional gradient. Non-zero abundances are shown in grey. The locations of the species optima are highlighted in bold

	Plot									
Species	**P1**	**P2**	**P3**	**P4**	**P5**	**P6**	**P7**	**P8**	**P9**	**P10**
S1	**0.15**	0	0	0	0	0	0	0	0	0
S2	**0.4**	0.2	0.15	0.05	0	0	0	0	0	0
S3	0.1	**0.15**	0.05	0	0	0	0	0	0	0
S4	0.2	**0.35**	0.25	0.15	0.05	0	0	0	0	0
S5	0	0	**0.1**	0	0	0	0	0	0	0
S6	0	0	0	**0.05**	0	0	0	0	0	0
S7	0.15	0.2	0.25	**0.35**	0.25	0.2	0.1	0.1	0.1	0
S8	0	0.1	0.15	0.25	**0.35**	0.3	0.2	0.1	0	0
S9	0	0	0.05	0.15	**0.25**	0.2	0.1	0	0	0
S10	0	0	0	0	0.1	**0.2**	0.15	0	0	0
S11	0	0	0	0	0	0	**0.15**	0	0	0
S12	0	0	0	0	0	0.1	0.25	**0.5**	0.45	0.45
S13	0	0	0	0	0	0	0.05	0.15	**0.25**	0.05
S14	0	0	0	0	0	0	0	0.1	0.15	**0.3**
S15	0	0	0	0	0	0	0	0.05	0.05	**0.2**

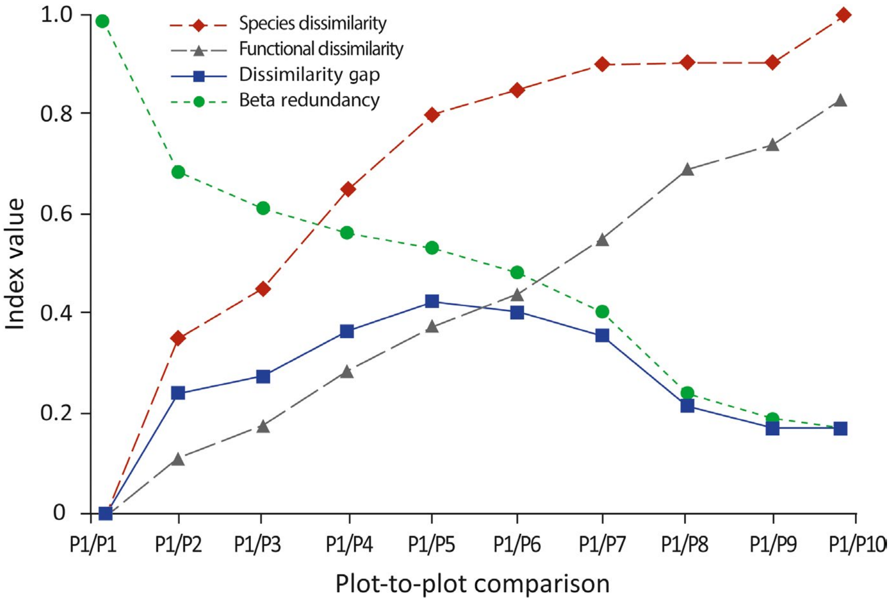

FIGURE 1 Profile diagram showing the response of species dissimilarity D_R, functional dissimilarity D_{KG}, dissimilarity gap $D_R - D_{KG}$ and beta redundancy $R_\beta = \left(D_R - D_{KG}\right)/D_R$ to changes in species composition along the artificial gradient in Table 1. The profile diagram reflects the comparison of the first plot with itself and all other plots along the gradient

At the other extreme, for two maximally dissimilar plots *P* and *Q* with no species in common and maximum functional dissimilarity $d_{ij} = 1$ for species *i* and *j* belonging to *P* and *Q*, respectively, we have $D_F = D_S = 1$ and hence $U_{PQ} = 1$. Likewise, since beta redundancy $R_\beta = 1 - U_\beta$ it follows that $R_{PP} = 1$ if $D_S = 0$, and $R_{PQ} = 0$ if $D_F = D_S = 1$.

4.2 | Vegetation primary succession

Caccianiga et al. (2006) showed that in the early-successional stage, the colonization of the moraine ridges of the Rutor glacier by the first pioneer species is primarily controlled by random dispersal, whereas the vegetation of the mid- and late-successional stages shows a higher level of functional homogeneity. This increase in functional homogeneity produces a similar increase in functional alpha and beta redundancy along the primary succession (Ricotta, de Bello, et al., 2016; Ricotta et al., 2020).

The results of the test for differences in the dispersion of D_R, D_{KG} and U_β among the three successional stages are shown in Table 3. First, based on the pairwise dissimilarities among pair of plots in each successional stage, the test calculates the dissimilarity of individual plots from the corresponding group centroid. Next, a permutational *t* test with 9,999 randomizations of these dissimilarities is used to test for pairwise differences in average dissimilarity of individual plots from their group centroids. For details on the PERMDISP test, see Anderson (2006).

In good agreement with the results of Ricotta et al. (2020), the successional stages do not differ significantly in species dissimilarity D_R, meaning that the species turnover among plots is more or less the same in all successional stages. By contrast, (non-standardized) functional dissimilarity D_{KG} and (standardized) uniqueness D_{KG}/D_R in the early-successional stage are both significantly higher than in the mid- and late-successional stages. That is, due to the more random dispersal mechanisms, in the early-successional stage, the species turnover is associated with a higher rate of functional turnover compared to the mid- and late-successional stages where the species in one plot tend to be replaced by functionally related species in the other plots.

TABLE 3 Mean (*SD*) dissimilarity values of the vegetation plots in each successional stage from the corresponding centroids. Pairwise differences in mean plot dissimilarity from the group centroids were tested with permutational *t* tests (9,999 permutations). For each dissimilarity index, numbers followed by the same letter do not differ significantly at $p < 0.05$. D_R = species dissimilarity; D_{KG} = functional dissimilarity; U_β = beta uniqueness

	Early-successional stage (17 plots)	Mid-successional stage (32 plots)	Late-successional stage (10 plots)
D_R	0.407 (0.075)^a	0.365 (0.083)^a	0.361 (0.106)^a
D_{KG}	0.149 (0.044)^a	0.095 (0.026)^b	0.091 (0.023)^b
U_β	0.253 (0.037)^a	0.182 (0.024)^b	0.170 (0.016)^b

5 | DISCUSSION

Ricotta et al. (2020) introduced the concept of beta redundancy to summarize the fraction of species dissimilarity D_S between two plots not expressed by functional or phylogenetic dissimilarity D_F. From an ecological viewpoint, this index tells us to what degree the species turnover between two plots is associated with a functional or phylogenetic turnover among the species in both plots. From a technical viewpoint, a necessary condition for a suitable index of beta redundancy is that the functional or phylogenetic dissimilarity is always lower than species dissimilarity: $D_F \le D_S$. This condition prevents beta redundancy from taking negative values. Ricotta et al. (2020) also developed a new class of indices of functional and phylogenetic dissimilarity between plots that conform to the redundancy property

$D_F \le D_S$. However, these indices depend on a hierarchical structure (a tree) of functional differences among species, which is not always considered adequate to portray the species functional relationships.

To develop a new index of functional beta redundancy that does not require the definition of a functional tree, our first step was to 'import' in the ecological literature an algorithmic index of functional dissimilarity D_{KG} originally proposed by Kosman (1996) and Gregorius et al. (2003) for genetic studies. Given two plots P and Q, the index is based on the optimal overall matching between the species abundances in both plots, so as to minimize the mean functional dissimilarity for the matched species abundances between P and Q. Since the calculation of D_{KG} does not require a tree-based species structure, the proposed measure of functional beta redundancy is now more flexible and compatible with the usual ways of representing functional relationships among species. Note that, since this index is essentially a kind of mean functional dissimilarity between the species in two plots, the practitioner can base the analysis on any functional dissimilarity measure of choice.

Being conform to the redundancy property $D_F \le D_S$, this algorithmic index enables to calculate (relative) functional redundancy and uniqueness in the usual way: $R_\beta = \left(D_S - D_F\right)/D_S$ and $U_\beta = 1 - R_\beta = D_F/D_S$. In addition to these relative coefficients, for a dissimilarity index that is bounded in the range [0, 1] the non-standardized coefficients of functional dissimilarity D_F and dissimilarity gap $D_S - D_F$ may be also used.

The main difference between beta redundancy and uniqueness and their non-standardized versions, $D_S - D_F$ and D_F, is how the measures are scaled. For two plots with relative abundance vectors $P = \left(p_1, \ldots, p_i, \ldots, p_S\right)$ and $Q = \left(q_1, \ldots, q_j, \ldots, q_S\right)$, a measure of non-standardized functional dissimilarity D_F in the range [0, 1], attains its maximum value (i.e. its global maximum) $D_F = 1$ for two maximally dissimilar plots with no species in common and maximum functional differences $d_{ij} = 1$ for species i belonging to plot P and species j to plot Q. By contrast, to calculate U_β functional dissimilarity D_F is scaled by its local maximum D_S, that is, by the maximum value that D_F can reach by keeping the relative abundance vectors unchanged and by imposing $d_{ij} = 1$ for all $i \ne j$.

The ecologically interesting aspect of the non-standardized dissimilarity gap $D_S - D_F$ is related to its dual nature. In fact, $D_S - D_F$ is at the same time a component of species *dissimilarity* and of functional *similarity*. The dissimilarity gap thus summarizes to what degree the differential species in two plots are able to perform the same ecological functions. Therefore, $D_S - D_F$ and its standardized version R_β are directly related to classical ecological processes, such as habitat filtering (Zobel, 1997), dark diversity (Pärtel et al., 2011) and the species carousel model (van der Maarel & Sykes, 1993).

For example, using simulated and real data, Laroche et al. (2020) illustrated how the difference between functional and compositional dissimilarities can help in identifying the processes underpinning diversity patterns at the metacommunity scale. In case of habitat filtering, species in the same habitat tend to have more similar traits that help them to cope with the local environmental conditions. Optimal traits are different from one habitat to another. Species present in the regional species pool but absent from a given habitat may thus have non-optimal traits for that habitat that enable them to colonize different habitats with different environmental conditions. If species traits are more related to their fitness than to their niche, then, competitive exclusion could lead to the absence of the less competitive species from a given site and thus to coexisting species with similar trait values. Combined together, these equalizing processes due to abiotic and biotic filtering (i.e. species share trait values that make them locally adapted to their environment and that ensure their similarity in terms of fitness; Chesson, 2000) could both lead to high D_S and D_F, low R_β and low $D_S - D_F$ between plots of different habitats, and to low D_F and relatively high to high R_β between plots of similar habitats depending on the level of the corresponding D_S.

If dispersal is high between plots regardless of habitat conditions, and if stabilizing niche differences (see Chesson, 2000) favour coexistence between species with distinct trait values allowing low overlap in resource use and stronger intraspecific competition than interspecific competition, then we expect high functional differences between locally coexisting species and high species turnover between plots because similar species cannot coexist. Accordingly, we also expect high functional overdispersion meaning that the functional differences within plots are high, and the plots are functionally similar because for each species in one plot we can expect to find a 'functionally relative' species not in the same plot but in another plot. In that case, limiting similarity due to stabilizing niche differences will lead to high D_S, low D_F, and hence high R_β and high $D_S - D_F$ between plots irrespective of the environmental conditions in the different plots.

High beta redundancy between plots (R_β and $D_S - D_F$), combined with high species dissimilarity (high D_S) could also inform priorities of conservation if some vulnerable species are absent in a site although the local ecological (biotic and abiotic) conditions would be favourable (dark diversity, Pärtel et al., 2011). This could be due to the species mobility and to stochastic colonization processes of favourable habitats (the species carousel of van der Maarel & Sykes, 1993). However, this could also be driven by habitat fragmentation, local extinction and limited or even hampered dispersal between the remnant habitat patches. This diversity of processes emphasizes the importance of selecting an appropriate null hypothesis for analysing beta-redundancy patterns. In this paper, we used a standard permutational approach. Narrower null hypotheses, such as constrained permutations (Peres-Neto et al., 2001) or the neutral baseline approach of Laroche et al. (2020) could also be used to facilitate the distinction between alternative processes that may produce similar species distribution patterns.

Temporal surveys, revealing increase in D_S over years, accompanied by an increase in R_β and $D_S - D_F$, could be even more informative alerting conservation agencies to potentially drastic environmental impact on biodiversity necessitating ecosystem restoration. Consider a hypothetical case where functional dissimilarities between plots in a habitat are proportional to species dissimilarities: the more complementary the plots are in terms of species, the more functional types they together contribute to the functional diversity of the habitat. If in addition local species extinctions are so numerous that some species become globally extinct (over all habitat patches), R_β is expected to remain constant but $D_S - D_F$ to decrease, meaning that the original levels of species and functional diversity could only be reestablished by habitat restoration and species reintroductions, wherever possible.

To conclude, functional beta redundancy allows us to explore an important aspect of the complex multidimensional space of ecological data. As highlighted by several authors (see e.g. Lavorel et al., 2008; Ricotta & Moretti, 2011), which traits are actually relevant for ecosystem functioning depends on the specific process of interest. Therefore, a critical point is the selection of an appropriate set of functional traits. The basic assumption for exploring the effects of dissimilarity on ecosystem functioning is that communities with similar functional traits have similar ecological properties. Therefore, two communities are supposed to be functionally similar with respect to some a priori-defined ecological property if they share the same traits. In principle, increasing the number of traits leads to more accurate measures of community similarity. However, these higher-dimensional functional spaces generally do not have any direct biological connection to the specific ecological properties under scrutiny. Therefore, instead of building increasingly larger functional spaces, we need to develop increasingly focused spaces that optimize their association with the property of interest (Ricotta & Moretti, 2010). The construction of such 'tailored' functional spaces may be based on expert knowledge (Caccianiga et al., 2006), statistical methods (Pierce et al., 2017; Ricotta & Moretti, 2010) or on modelling approaches (Petchey & Gaston, 2006). In this view, we believe that future work combining indices of beta redundancy with the development of functional spaces strongly connected to a priori-selected properties will greatly contribute to the understanding of the relationships among different facets of community dissimilarity and ecosystem functioning.

AUTHORS' CONTRIBUTIONS

C.R. and S.P. formulated the research problem; E.K. and F.L. provided important feedback which helped shape the research; C.R. and S.P. analysed the data; C.R. took the lead in writing the manuscript and S.P. in writing the appendices. All authors revised the manuscript critically and approved the final version.

DATA AVAILABILITY STATEMENT

The R code used in this paper is deposited in the Dryad Digital Repository https://doi.org/10.5061/dryad.b2rbnzsds (Ricotta et al., 2021). The data of the Alpine vegetation are available online in the R package ADIV https://cran.r-project.org/web/packages/adiv/index.html (R Core Team, 2021). The functional dissimilarity matrix of the artificial data set is available in the Supporting Information of this paper (Appendix S2).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Appendix 1. Proof that the algorithmic dissimilarity D_{KG} is always not higher than the Rogers dissimilarity D_R.

Let p_i and q_i be the relative abundances of species *i* in plots *P* and *Q*, respectively, such that $0 \le p_i \le 1$, $0 \le q_i \le 1$ and $\sum_i^S p_i = \sum_i^S q_i = 1$, where *S* is the total number of species in both plots, and Δ be a symmetric $S \times S$ matrix of pairwise functional dissimilarities d_{ij} between species *i* and *j* $(i, j = 1, 2, ..., S)$ in the range $[0,1]$ with $d_{ij} = d_{ji}$ and $d_{ii} = 0$.

We define a matching between plots *P* and *Q* as a matrix *M* with dimension $S \times S$ and coefficients in $[0,1]$ such as:

$$\begin{aligned} &\forall j \in \{1,...,S\}, \sum_{i=1}^{S} M_{ij} = p_j \\ &\forall i \in \{1,...,S\}, \sum_{j=1}^{S} M_{ij} = q_i \end{aligned} \qquad (1.1)$$

We define the dissimilarity between *P* and *Q* associated to the matching *M* and the dissimilarity matrix Δ as:

$$D(M, \Delta) = \sum_{i=1}^{S} \sum_{j=1}^{S} M_{ij} \Delta_{ij} \qquad (1.2)$$

The set of possible matching pairs between *P* and *Q* is a closed and bounded subset of the $S \times S$ matrices. Consequently, the algorithmic dissimilarity D_{KG} between *P* and Q can be defined as $D_{KG}(\Delta) = \min_M D(M, \Delta)$ and there exists an admissible matching $M_{KG}(\Delta)$ such that $D_{KG}(\Delta) = D(M_{KG}(\Delta), \Delta)$

Denoting with Δ^* the dissimilarity matrix with $\Delta^*_{ii} = 0$ and $\Delta^*_{ij} = 1$ for $i \ne j$, we will prove that $D_{KG}(\Delta) \le D_{KG}(\Delta^*)$ for all dissimilarity matrices Δ.

Proof

Let Δ be a dissimilarity matrix.

a) Because $d_{ij} \le 1$ for all $i \in \{1,...,S\}$ and $j \in \{1,...,S\}$, it is straightforward that $D(M, \Delta) \le D(M, \Delta^*)$ for all matchings *M* and all dissimilarity matrices Δ. This implies that $D(M_{KG}(\Delta^*), \Delta^*) \ge D(M_{KG}(\Delta^*), \Delta)$ and thus $D_{KG}(\Delta^*) \ge D(M_{KG}(\Delta^*), \Delta)$.

b) As $D_{KG}(\Delta) = \min_M D(M, \Delta)$, by definition $D_{KG}(\Delta) \le D(M_{KG}(\Delta^*), \Delta)$.

a) and b) imply $D_{KG}(\Delta) \le D_{KG}(\Delta^*)$.

End of proof

It has been shown by Kosman (2014) that $D_{KG}\left(\Delta^*\right)$ equals the Rogers dissimilarity between plots *P* and *Q*, denoted D_R. Thus we proved that for any dissimilarity matrix Δ, $D_{KG}\left(\Delta\right) \le D_R$.

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Appendix 2. Interspecies dissimilarity matrix used for the calculation of the proposed redundancy measures with the artificial data in Table 1.

Species	S1	S2	S3	S4	S5	S6	S7	S8	S9	S10	S11	S12	S13	S14	S15
S1	0	0.1	0.2	0.2	0.3	0.4	0.4	0.5	0.5	0.6	0.7	0.8	0.9	1	1
S2	0.1	0	0.2	0.2	0.3	0.4	0.4	0.5	0.5	0.6	0.7	0.8	0.9	1	1
S3	0.2	0.2	0	0.1	0.2	0.3	0.3	0.4	0.4	0.5	0.6	0.7	0.8	0.9	0.9
S4	0.2	0.2	0.1	0	0.2	0.3	0.3	0.4	0.4	0.5	0.6	0.7	0.8	0.9	0.9
S5	0.3	0.3	0.2	0.2	0	0.2	0.2	0.3	0.3	0.4	0.5	0.6	0.7	0.8	0.8
S6	0.4	0.4	0.3	0.3	0.2	0	0.1	0.2	0.2	0.3	0.4	0.5	0.6	0.7	0.7
S7	0.4	0.4	0.3	0.3	0.2	0.1	0	0.2	0.2	0.3	0.4	0.5	0.6	0.7	0.7
S8	0.5	0.5	0.4	0.4	0.3	0.2	0.2	0	0.1	0.2	0.3	0.4	0.5	0.6	0.6
S9	0.5	0.5	0.4	0.4	0.3	0.2	0.2	0.1	0	0.2	0.3	0.4	0.5	0.6	0.6
S10	0.6	0.6	0.5	0.5	0.4	0.3	0.3	0.2	0.2	0	0.2	0.3	0.4	0.5	0.5
S11	0.7	0.7	0.6	0.6	0.5	0.4	0.4	0.3	0.3	0.2	0	0.2	0.3	0.4	0.4
S12	0.8	0.8	0.7	0.7	0.6	0.5	0.5	0.4	0.4	0.3	0.2	0	0.2	0.3	0.3
S13	0.9	0.9	0.8	0.8	0.7	0.6	0.6	0.5	0.5	0.4	0.3	0.2	0	0.2	0.2
S14	1	1	0.9	0.9	0.8	0.7	0.7	0.6	0.6	0.5	0.4	0.3	0.2	0	0.1
S15	1	1	0.9	0.9	0.8	0.7	0.7	0.6	0.6	0.5	0.4	0.3	0.2	0.1	0

Appendix 3. R scripts

The R function `"betaUniqueness"` calculates plot-to-plot uniqueness and redundancy taking account of functional dissimilarities between species using equation 5 and 6 in the main text. The R function `"dislptransport"` calculates the D_{KG} measure of dissimilarity (Kosman 1996; Gregorius et al. 2003) applied here to functional differences between plots (eq. 3 in the main text). This program is free software: you can redistribute it and/or modify it under the terms of the GNU General Public License http://www.gnu.org/licenses/.
It will be integrated in version 2.1 of the adiv package of R: https://cran.r-project.org/web/packages/adiv/index.html. The functions were checked and applied with R-4.0.2.

Disclaimer: users of this code are cautioned that, while due care has been taken and it is believed accurate, it has not been rigorously tested and its use and results are solely the responsibilities of the user.

Dependencies: lpSolve (Berkelaar et al. 2020).

Function Syntax:

```
betaUniqueness <- function (comm, dis, Nind = 10000)
{
    if (!(inherits(comm, "data.frame") | inherits(comm, "matrix")))
        stop("comm is not a data.frame or a matrix")
    if(nrow(comm) < 2) stop("comm must have at least two rows")
    D <- as.matrix(dis)
    if (any(D > 1)) {
        D <- D/max(D)
        warnings("All values in dis have been divided by their maximum
(highest observed value)")
    }
    U <- dislptransport(comm, D, diag = FALSE, upper = FALSE, Nind = Nind)
    dis0 <- matrix(1, ncol(comm), ncol(comm))-diag(rep(1, ncol(comm)))
    U0 <- dislptransport(comm, dis0, diag = FALSE, upper = FALSE, Nind =
Nind)
    Ustar <- U0
    Ustar[Ustar<=0] <- 1
    res <- list()
    res$betaUniqueness <- as.matrix(U/Ustar)
    res$betaRedundancy <- 1 - as.matrix(U/Ustar)
    res$dissimilarityGap <- as.matrix(U0-U)
    res$DR <- as.matrix(U0)
    res$DKG <- as.matrix(U)
    return(res)
}

dislptransport <-
function (comm, dis, diag = FALSE, upper = FALSE, Nind = 10000)
{

    if (!(inherits(comm, "data.frame") | inherits(comm, "matrix")))
        stop("comm is not a data.frame or a matrix")
    if(nrow(comm) < 2) stop("comm must have at least two rows")
    D <- as.matrix(dis)
    nlig <- nrow(comm)
    ncol <- ncol(comm)
    d <- matrix(0, nlig, nlig)
    d.names <- row.names(comm)
```

```
    df <- as.data.frame(t(comm))
    dfp <- t(t(df)/colSums(df))
    funlp <- function(x) {
        row_rhs <- round(dfp[,x[1]] * Nind)
        if(sum(row_rhs) < Nind) {
            nmiss <- Nind - sum(row_rhs)
            e <- sample((1:nrow(dfp))[row_rhs < dfp[,x[1]] * Nind], nmiss)
            for(i in e)    row_rhs[i] <- row_rhs[i] + 1
        }
        if(sum(row_rhs) > Nind) {
            ntoo <- abs(Nind - sum(row_rhs))
            e <- sample((1:nrow(dfp))[row_rhs > dfp[,x[1]] * Nind], ntoo)
            for(i in e)    row_rhs[i] <- row_rhs[i] - 1
        }
        col_rhs <- round(dfp[,x[2]] * Nind)
        if(sum(col_rhs) < Nind) {
            nmiss <- Nind - sum(col_rhs)
            e <- sample((1:nrow(dfp))[col_rhs < dfp[,x[2]] * Nind], nmiss)
            for(i in e)    col_rhs[i] <- col_rhs[i] + 1
        }
        if(sum(col_rhs) > Nind) {
            ntoo <- abs(Nind - sum(col_rhs))
            e <- sample((1:nrow(dfp))[col_rhs > dfp[,x[2]] * Nind], ntoo)
            for(i in e)    col_rhs[i] <- col_rhs[i] - 1
        }
        row_signs <- rep("<=", ncol)
        col_signs <- rep(">=", ncol)
        res <- sum(lp.transport(D, "min", row_signs, row_rhs, col_signs,
col_rhs)$solution*D/Nind)
       return(res)
    }
    index <- cbind(col(d)[col(d) < row(d)], row(d)[col(d) < row(d)])
    d <- unlist(apply(index, 1, funlp))
    attr(d, "Size") <- nlig
    attr(d, "Labels") <- d.names
    attr(d, "Diag") <- diag
    attr(d, "Upper") <- upper
    attr(d, "method") <- "GregoriusGilletZiehe"
    attr(d, "call") <- match.call()
    class(d) <- "dist"
    return(d)
}
```

Usage: `betaUniqueness <- function (comm, dis, Nind = 10000)`
`dislptransport(comm, dis, diag = FALSE, upper = FALSE, Nind = 10000)`

Arguments:

`comm`: a matrix of *N* plots × *S* species containing the relative or absolute abundance of all species. Columns are species and plots are rows.

`dis`: a matrix or an object of class dist providing the functional dissimilarities between species (dissimilarities are nonnegative, symmetric, and the dissimilarity between a species and itself is zero). ***Species here must be in the same order as in the columns of comm***.

`Nind`: an integer. The algorithmic index will be applied by assuming that each plot contains `Nind` individuals. The highest `Nind`, the most precise the index value will be (see Gregorius et al. 2003, for more details).

`diag`: a logical value indicating whether the diagonal of the distance matrix should be printed by `'print.dist'`.

`upper`: a logical value indicating whether the upper triangle of the distance matrix should be printed by `'print.dist'`.

Value:

The function `dislptransport` returns a matrix with the values of the dissimilarity index D_{KG} for each pair of plots. The function `betaUniqueness` returns a list with the following objects:

`betaUniqueness`: a matrix with the values of the proposed beta uniqueness ($U_\beta=D_{KG}/D_R$) for each pair of plots (main text, eq. 6).

`betaRedundancy`: a matrix with the values of the proposed beta redundancy ($R_\beta=1-D_{KG}/D_R$) for each pair of plots (main text, eq. 5).

`dissimilarityGap`: a matrix with the values of the dissimilarity gap index (D_R-D_{KG}) for each pair of plots.

`DR`: a matrix with the values of the species-based (Rogers) dissimilarity index (D_R) for each pair of plots (main text, eq. 4).

`DKG`: a matrix with the values of the algorithmic functional dissimilarity index (D_{KG}) for each pair of plots (main text, eq. 3).

Example:

Install and load packages `lpSolve, vegan` and `adiv`.

```
install.packages("lpSolve")
install.packages("adiv") # Pavoine (2020a,b)
install.packages("vegan") # Oksanen et al. (2019)

library(lpSolve)
library(adiv)
library(vegan)
```

Load the dataset `RutorGlacier` in the adiv package of R.

```
data(RutorGlacier)
```

`RutorGlacier` is a list of several tables and a vector. The table named `'Abund'` contains the abundance of plant species in plots. The species traits are in another table named `'Traits'`.

In `RutorGlacier$Abund`, plots are in rows and species in columns.

Here the functional distances between species are calculated as in the main text as the Euclidean distance applied to species' traits, each standardized to zero mean and unit standard deviation :

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

Then the resulting functional distances among species were scaled to the unit range by dividing each distance by the maximum value in the distance matrix :

```
fundis <- fundis/max(fundis)
```

Load functions `betaUniqueness and dislptransport` in R. To apply function `betaUniqueness` to the Rutor Glacier dataset, use the following command:

```
frameDKG <- betaUniqueness(RutorGlacier$Abund, fundis)
```

The plot-to-plot values of functional beta uniqueness are:

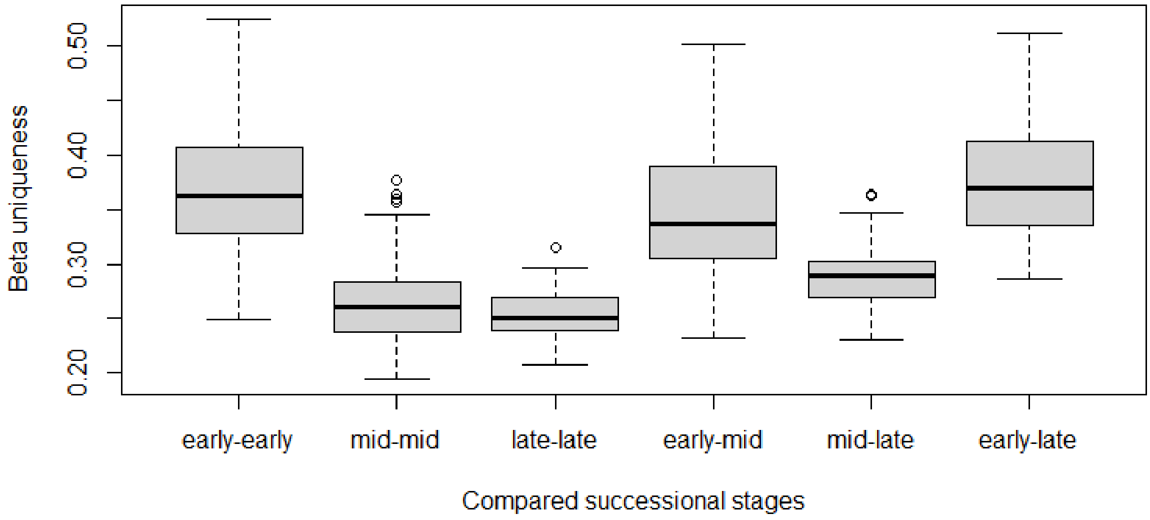
```
betaU_A <- frameDKG$betaUniqueness
```

and the plot-to-plot values of functional beta redundancy are:

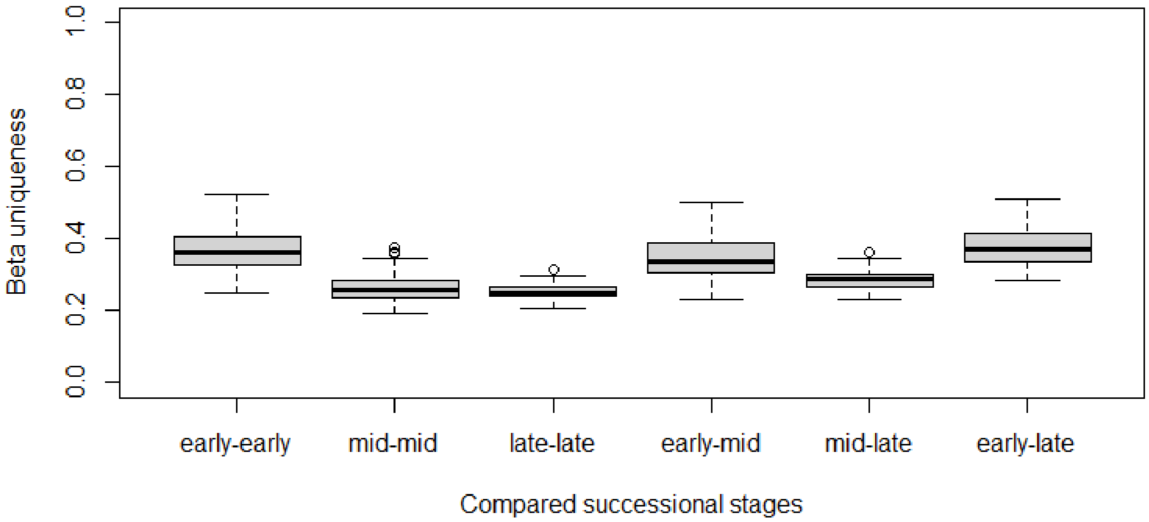
```
betaR_A <- frameDKG$betaRedundancy
```

In `RutorGlacier`, the object named `'Fac'` indicates which level of the successional gradient a given plot belongs to ("early" = early-successional stage, "mid" = mid-successional stage and "late" = late-successional stage). We use `Fac` below to display the functional beta uniqueness between two plots of the same successional stage, and between two plots of distinct successional stages.

```
f1 <- unlist(sapply(1:58, function(i) rep(RutorGlacier$Fac[i], 59-i)))
f2 <- unlist(sapply(1:58, function(i) RutorGlacier$Fac[-(1:i)]))
f <- paste(f1, f2, sep="-")
F <- factor(f, levels=c("early-early", "mid-mid", "late-late", "early-mid",
"mid-late", "early-late"))

vbetaU_A <- as.vector(as.dist(betaU_A))

boxplot(vbetaU_A~F, ylab="Beta uniqueness", xlab="Compared successional
stages")
```

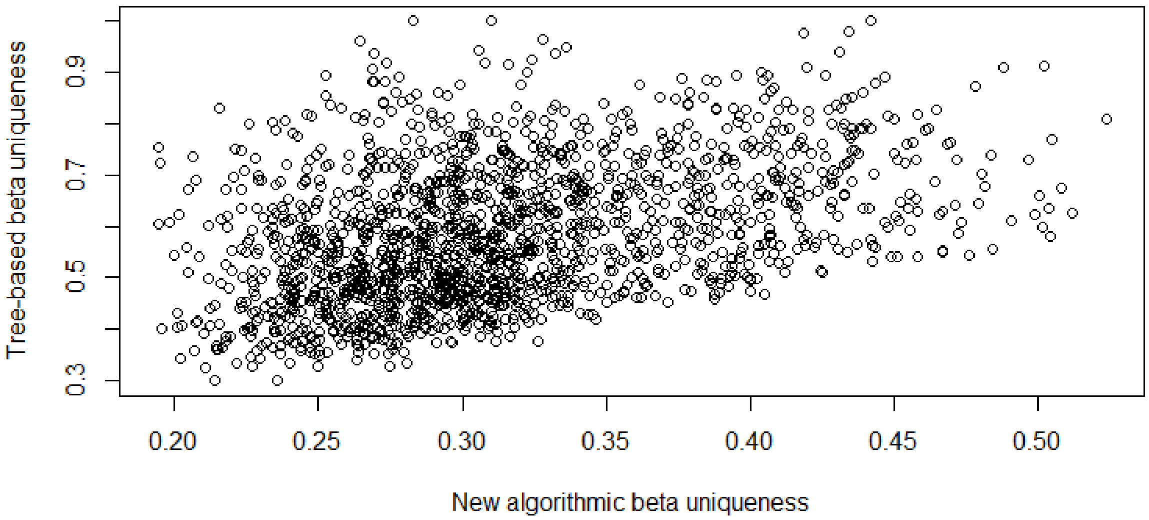


```
boxplot(vbetaU_A~F, ylab="Beta uniqueness", ylim=c(0,1), xlab="Compared
successional stages") # change of scale for the Y axis
```



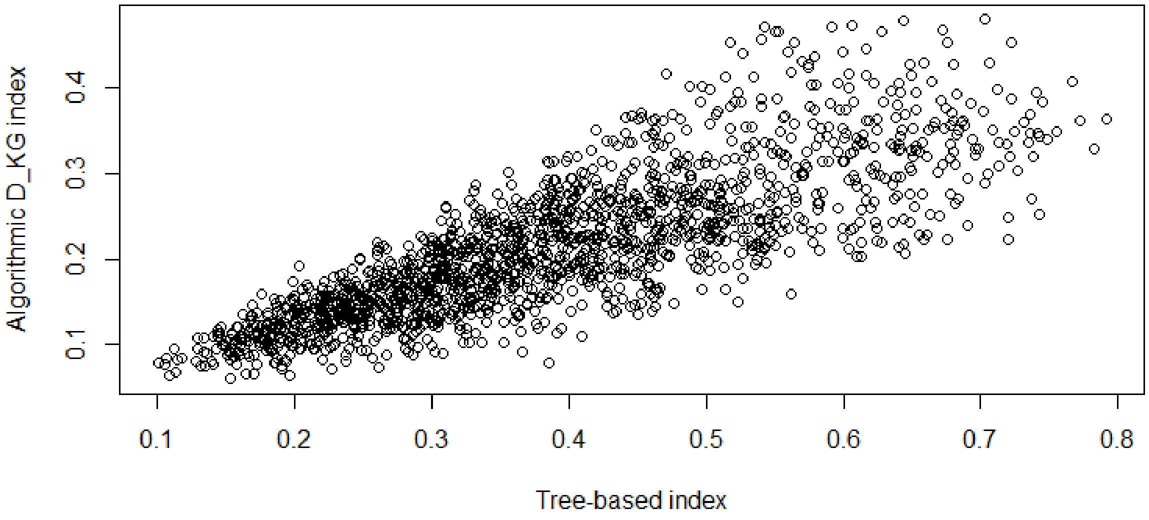
Below, we calculate Ricotta et al. (2020) tree-based index of beta functional uniqueness and compare the results with those provided by the new algorithmic index.

```
H <- hclust(fundis, "average")
Up <- betaTreeUniqueness(H, RutorGlacier$Abund, tol=0.00001)
vUp <- as.vector(as.dist(Up))


plot(vbetaU_A,  vUp,  xlab="New  algorithmic  beta  uniqueness",  ylab  ="Tree-
based beta uniqueness")
```



These beta uniqueness indices rely on plot-to-plot dissimilarity indices. Below, we compare the plot-to-plot dissimilarity indices: the tree-based index (Ricotta et al. 2020, function `DP` in package `adiv`) and Kosman (1996) & Gregorius et al. (2003) algorithmic index (D_{KG} in the main text; calculated above and stored in the list named `frameDKG`).

```
disKG <- as.dist(frameDKG$DKG)
disTree <- DP(H, RutorGlacier$Abund)

plot(as.vector(disTree), as.vector(disKG), xlab = "Tree-based index",
ylab="Algorithmic D_KG index")
```



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