Measuring functional dissimilarity among plots: adapting old methods to new questions

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Author contribution statement CR formulated the idea. SP and CR developed the methodology. SP wrote the R code and analyzed the data. SP and CR wrote the manuscript.

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Abstract Ecologists routinely use dissimilarity measures between pairs of plots to explore the complex mechanisms that drive community assembly. Traditional dissimilarity measures usually quantify plot-to-plot dissimilarity based either on species presences and absences within plots or on species abundances, thus assuming that all species are equally and maximally distinct from one another. However, the value of dissimilarity measures that incorporate information on functional differences among species is becoming increasingly recognized. Since these 'functional dissimilarity measures' have been developed for capturing new aspects of plot-to-plot dissimilarity, they have usually little to do with more traditional measures based solely on species incidence or abundance data. In this paper we introduce a general method for adapting a large family of traditional dissimilarity coefficients to the measurement of functional differences among plots. The behavior of the proposed method, for which we provide a simple R function, was evaluated with published data on plant communities in a coastal marsh plain in Algeria. As shown by the worked example, our proposal produces a coherent framework for summarizing functional dissimilarity among plots. Being based on a generalization of classical dissimilarity measures with well-known properties, this new family of functional dissimilarity indices also has a great potential for future theoretical and applied developments in this field of research.

Keywords: Branching property; Bray-Curtis dissimilarity; Species ordinariness; Sum property.

1. Introduction

Ecologists have developed a multitude of (dis)similarity measures between pairs of plots (or communities, assemblages, relevés, sites, quadrats, etc.) for exploring various aspects of the complex mechanisms that drive community assembly (see e.g. Orlóci 1978; Podani 2000; Legendre and Legendre 2012). These measures usually quantify plot-to-plot dissimilarity based either on species incidence or abundance within plots, thus assuming that all species are equally and maximally distinct from one another, while neglecting information on functional differences among species.

More recently, a number of ‘functional dissimilarity measures’ have been proposed for summarizing different facets of functional differences among plots (Rao 1982; Clarke and Warwick 1998; Izsák and Price 2001; Champely and Chessel 2002; Pavoine et al. 2004; Chiu et al. 2014; Pavoine and Ricotta 2014; Ricotta et al. 2016). Such new dissimilarity measures incorporate information on the species functional traits. Therefore, they are expected to correlate more strongly with ecosystem-level processes, as species influence these processes via their traits (Mason and de Bello 2013). Since functional dissimilarity measures have been developed for capturing new aspects of ecological differences among plots, they are usually not directly related to more traditional measures of species turnover which are based solely on species incidence or abundance data.

The aim of this paper is thus to introduce a methodological framework for adapting a large family of traditional dissimilarity coefficients to the measurement of functional differences among plots. The main advantage of this approach is that being based on a generalization of well-known dissimilarity measures which have been extensively used in ecology for a long time, these new functional measures benefit from decades of research on multivariate resemblance.

2. Methods

2.1. A general family of traditional dissimilarity measures

Let U and V be two plots where x_{Uj} and x_{Vj} are the abundance values of species j in plots U and V , respectively, and N is the total number of species sampled in both plots (i.e. the species for which $\min\{x_{Uj}, x_{Vj}\} > 0$). A desirable property for a dissimilarity coefficient is the so-called ‘sum property’ (Ricotta and Podani 2017). That is, its ability to be additively partitioned into species-level contributions thus enabling to emphasize the relevance of single species to plot-to-plot dissimilarity.

Among the many dissimilarity measures that conform to the sum property, the Canberra distance (Lance and Williams 1967) is obtained by standardizing separately for each species the absolute difference in species abundances by the sum of the abundances in both plots:

78

$$79 \quad CD = \sum_{j=1}^N \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (1)$$

80

81 The Canberra distance is bounded between 0 and N . Therefore, a normalized measure in the
82 range $[0,1]$ is obtained by division by N :

83

$$84 \quad NC = \frac{1}{N} \sum_{j=1}^N \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (2)$$

85

86 On the other hand, the dissimilarity coefficient proposed by Bray and Curtis (1957), one of the
87 most popular measures of compositional dissimilarity among ecologists, implies normalization of
88 the sum of species-wise differences by the total abundance of species in both plots:

89

$$90 \quad BC = \frac{\sum_{j=1}^N |x_{Uj} - x_{Vj}|}{\sum_{j=1}^N (x_{Uj} + x_{Vj})} \quad (3)$$

91

92 To emphasize the relationship between the Bray-Curtis dissimilarity and the Canberra distance,
93 we can rewrite BC as:

94

$$95 \quad BC = \sum_{j=1}^N \frac{|x_{Uj} - x_{Vj}|}{\sum_{k=1}^N (x_{Uk} + x_{Vk})} = \sum_{j=1}^N w_j \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (4)$$

96

97 where

98

$$99 \quad w_j = (x_{Uj} + x_{Vj}) / \sum_{k=1}^N (x_{Uk} + x_{Vk}) \quad (5)$$

100

101 with $0 \leq w_j \leq 1$ and $\sum_{j=1}^N w_j = 1$.

102 As shown by Eq. (4), the Bray-Curtis dissimilarity can be expressed as a normalized form of the
103 Canberra distance in which the contribution of species j to overall dissimilarity
104 $|x_{Uj} - x_{Vj}| / (x_{Uj} + x_{Vj})$ is weighted by the relative abundance of j in plots U and V . Based on the

105 observed relationship between the Bray-Curtis dissimilarity and the normalized Canberra distance,
 106 Ricotta and Podani (2017) defined a ‘generalized Canberra dissimilarity’ which includes *BC* and
 107 *NC* as special cases:

$$109 \quad GC = \sum_{j=1}^N \pi_j \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (6)$$

110
 111 with $0 \leq \pi_j \leq 1$ and $\sum_{j=1}^N \pi_j = 1$. The weights π_j may be related to any species-specific ecological
 112 variable that is assumed to influence ecosystem functioning, such as the species phylogenetic and/or
 113 functional originality, or their conservation value. For $\pi_j = 1/N$, we obtain the normalized
 114 Canberra distance, while setting $\pi_j = w_j$, we obtain the Bray-Curtis dissimilarity.

115 Going a step further, we can define an even larger family of dissimilarity coefficients as:

$$117 \quad D_{\pi} = \sum_{j=1}^N \pi_j d(x_{Uj}, x_{Vj}) \quad (7)$$

118
 119 where the term $d(x_{Uj}, x_{Vj})$ represents the single-species dissimilarity of *U* and *V* for species *j* in the
 120 range [0, 1].

121 Members of this family are the generalized version of the Marczewski-Steinhaus coefficient
 122 (Ricotta and Podani 2017):

$$124 \quad D_{MS} = \sum_{j=1}^N \pi_j \frac{|x_{Uj} - x_{Vj}|}{\max\{x_{Uj}, x_{Vj}\}} \quad (8)$$

125
 126 or the evenness-based dissimilarity coefficients proposed by Ricotta (2018):

$$128 \quad D_{EVE} = \sum_{j=1}^N \pi_j (1 - EVE_j) \quad (9)$$

129
 130 where EVE_j is a measure of the evenness of species *j* in plots *U* and *V*. For example, EVE_j can be
 131 obtained with Pielou’s evenness:

$$EVE_j = H_j / \log 2 \quad (10)$$

134

135 where H_j is the Shannon entropy of species j : $H_j = -\frac{x_{Uj}}{x_{Uj} + x_{Vj}} \log \left(\frac{x_{Uj}}{x_{Uj} + x_{Vj}} \right) - \frac{x_{Vj}}{x_{Uj} + x_{Vj}} \log \left(\frac{x_{Vj}}{x_{Uj} + x_{Vj}} \right)$.

136 In the next sections, we will show how to apply this family of dissimilarity coefficients to the
137 measurement of functional dissimilarity among plots.

138

139 2.2. A new family of functional dissimilarity measures

140 Regardless of how pairwise functional differences among species i and j are calculated, they are
141 usually represented by symmetric dissimilarity coefficients δ_{ij} with $\delta_{ij} = \delta_{ji}$ and $\delta_{ii} = 0$. If δ_{ij} is
142 bounded in the range $[0, 1]$, we can derive a corresponding similarity coefficient $\sigma_{ij} = 1 - \delta_{ij}$ as the
143 complement of δ_{ij} . Note that dissimilarity measures with an upper bound $\delta_{\max} > 1$ can be
144 normalized by dividing each term by $\delta_{\max}$, while for dissimilarity measures without an upper bound
145 we can still get a locally normalized dissimilarity in the range $[0, 1]$ by dividing each term by the
146 maximum value in the data set.

147 Combining species abundances x_{Uj} and between-species similarities σ_{ij} , Leinster and Cobbold
148 (2012) defined the ‘ordinariness’ of species j as the abundance of all species in plot U that are
149 functionally similar to j such that:

150

$$z_{Uj} = \sum_{i=1}^N x_{Ui} \sigma_{ij} \quad (11)$$

152

153 where z_{Uj} is the abundance of all species that are functionally similar to j (including j itself). For
154 species j , z_{Uj} thus measures the commonness of all individuals in plot U that support the functions
155 associated with j . z_{Uj} ranges from x_{Uj} if all species $i \neq j$ are maximally dissimilar from j , such that
156 $\sigma_{ij} = 0$, to $\sum_{i=1}^N x_{Ui}$ (i.e. the total species abundance in plot U) if all species $i \neq j$ are functionally
157 identical to j such that $\sigma_{ij} = 1$. Hence, the abundance of species similar to j is at least as great as the
158 abundance of j itself.

159 Given two functionally identical plots U and V , we have that for each species in U and V , the
160 ordinariness $z_{Uj} = \sum_{i=1}^N x_{Ui} \sigma_{ij}$ in plot U is equal to the corresponding value $z_{Vj} = \sum_{i=1}^N x_{Vi} \sigma_{ij}$ in plot
161 V . In other words, for two functionally identical plots, the abundance of the species similar to j in

plot U is equal to the abundance of the species similar to j in plot V (for definitions and proofs see Appendix 1). In contrast, for two maximally distinct assemblages, either z_{Uj} or z_{Vj} is equal to zero, meaning that the species in plot U do not have any functional analogue in plot V .

Hence, in principle, we could calculate a measure of functional dissimilarity among plots with any of the many traditional dissimilarity measures developed for species abundance data by simply replacing the species abundances x_{Uj} and x_{Vj} in both plots with their corresponding species ordinariness z_{Uj} and z_{Vj} . The resulting measures meet the foremost requirements for a dissimilarity coefficient in the range $[0, 1]$: for two maximally dissimilar plots (i.e. two plots with no species in common and $\sigma_{ij} = 0$ for species i belonging to the first plot and species j to the second plot), the measure takes the value one, whereas for two functionally identical plots the measure takes the value zero (see Pavoine and Ricotta 2014).

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2.3. An additional requirement for functional dissimilarity

A potential drawback of this approach is that the dissimilarity indices obtained by substituting the species abundances x_{Uj} and x_{Vj} in U and V with the species ordinariness z_{Uj} and z_{Vj} tend to overemphasize the relevance of the most functionally redundant species. For example, consider two plots U and V and two maximally dissimilar species i and j with $\sigma_{ij} = 0$. Plot U contains species i with abundance $x_{Ui} = 5$ and species j also with abundance $x_{Uj} = 5$, while plot V contains only species j with abundance $x_{Vj} = 10$:

181

	i	j
Plot U	5	5
Plot V	0	10

182

Since the two species are maximally dissimilar, their ordinariness is identical to their abundances: $x_{Ui} = z_{Ui} = 5$, $x_{Uj} = z_{Uj} = 5$, and $x_{Vj} = z_{Vj} = 10$. Therefore, using the species ordinariness for calculating the functional dissimilarity between U and V with the Bray-Curtis coefficient (see Eq. 3), we obtain $BC_z = 0.5$.

However, if we split species i into two functionally identical species i' and i'' , each with abundance $x_{Ui'} = x_{Ui''} = 2.5$ and $\sigma_{i'i''} = 1$:

189

190

	i'	i''	j
Plot U	2.5	2.5	5
Plot V	0	0	10

we have $z_{U i'} = z_{U i''} = 5$, $z_{U j} = 5$ and $z_{V j} = 10$. Accordingly, $BC_z = 0.6$, whereas, intuitively, the functional dissimilarity between U and V should not change if one species is replaced by two identical species with the same total abundance.

More generally, irrespective of the values of the pairwise similarities among species pairs, the species ordinariness overemphasizes the role of the functionally redundant species in both plots. If the species in U are functionally similar to the species in V , the similarity between U and V will be exaggerated. To the contrary, if the species in U are functionally different from the species in V , the similarity between U and V will be excessively reduced.

Therefore, a meaningful measure of functional dissimilarity between pairs of plots needs to conform to the following branching requirement: the value of functional dissimilarity among a pair of plots U and V should not change if a given species j is replaced by two functionally identical species with the same total abundance of j in U and V .

In Appendix 1, we show that a special case of the general family of dissimilarity coefficients D_π conforms to this additional requirement. If the single-species dissimilarities d in Eq. (7) are calculated from the species ordinariness z_{Uj} , while the weighting factors w_j are calculated from the original species abundances $w_j = (x_{Uj} + x_{Vj}) / \sum_{k=1}^N (x_{Uk} + x_{Vk})$, we get a family of measures:

$$D_w = \sum_{j=1}^N w_j d(z_{Uj}, z_{Vj}) \quad (12)$$

which conforms to the branching requirement for functional dissimilarity coefficients (proof in Appendix 1):

Take for example the generalized version of the Bray-Curtis coefficient. If this measure is calculated as $BC_w = \sum_{j=1}^N w_j |z_{Uj} - z_{Vj}| / (z_{Uj} + z_{Vj})$, it is easily shown that BC_w conforms to the branching requirement. The same holds for all functional dissimilarity coefficients that can be expressed according to Eq. (12).

3. Worked example

We analyzed the functional composition of plant communities in the coastal marsh plain of La Mafragh (36°48' N–008°00' E) in Algeria. Detailed information on the data set can be found in de

221 Bélair (1981) and Pavoine et al. (2011). The area is a basin filled by alluvial and colluvial deposits
222 and furrowed by rivers. The lowest parts are composed of large and small marshes. The study area
223 is bounded by dunes with a narrow connection (Oued Mafragh) to the Mediterranean Sea in the
224 north (north is at the top of the panels), by Numidian clay-sandstone mountains in the south, by a
225 river (Oued El Kebir) in the east, and by an irrigated agricultural zone in the west. It is about 15km
226 large from east to west and 8km from north to south.

227 97 study sites were regularly distributed on the plain. de Bélair (1981) collected species
228 abundances and environmental data (de Bélair 1981), and Pavoine et al. (2011) collected species
229 traits from the literature. As in Pavoine et al. (2011), we focused our analyses on four traits: life
230 cycle (categorical multichoice variable with four levels [perennial; annual; biennial; seasonal]),
231 pollination (categorical multichoice variable with three levels [autogamous, entomogamous,
232 anemogamous]), presence of spiky structures (ordinal variable with three levels [0 = no; 1 =
233 sometimes; 2 = yes]), and hairy leaves (ordinal variables with three levels [0 = no; 1 = sometimes; 2
234 = yes]). We calculated the functional dissimilarities between species as the average dissimilarity
235 over all traits (see Pavoine et al. 2009). We used the Sørensen index for categorical multichoice
236 traits and the Euclidean distance on rank-transformed ordinal variables.

237 To obtain species-based dissimilarities among plots, we applied the traditional Bray-Curtis
238 dissimilarity (Eq. 4) to the species relative abundances. Then, to obtain functional dissimilarities
239 among plots, we applied the functional version of the Bray-Curtis dissimilarity to the species
240 ordinariness z_{ij} (see Eq. 12). We then analyzed these plot-to-plot dissimilarities with Principal
241 Coordinate Analysis (PCoA) after Cailliez (1983) transformation. This operation consists in adding
242 the smallest constant to all dissimilarities to make the resulting dissimilarity matrix Euclidean. We
243 finally compared the results obtained from the PCoA with the spatial distribution of eight
244 environmental variables (Fig. 1): elevation [m], clay [%], silt [%], sand [%], K₂O [%], Mg²⁺ [mEq/
245 100g], Na⁺ [mEq/100 g], K⁺ [mEq/100g]. The R scripts developed for this analysis are provided in
246 Appendix 2.

247

248 4. Results

249 We retained the first axis of the PCoA applied to plot-to-plot functional dissimilarities (Fig. 2) as
250 its eigenvalue is about five-fold that of the second axis (Fig. 3). The high number of eigenvalues
251 close to 0.006 in this analysis (Fig. 3A) is due to the Cailliez transformation used to render the
252 dissimilarities Euclidean. Similar patterns were also obtained using non-metric Multidimensional
253 Scaling (Appendix 2), meaning that the results were not affected by the ordination method used for
254 analyzing the data. According to Figure 1 and 2, the negative part of the PCoA axis corresponded

mainly to plots at lower elevation in the middle of the study area where clay-rich soils had high concentrations of K^+ , Mg^{++} , Na^+ and K_2O , indicating high salinity. On the other hand, plots with positive coordinates tended to be located at higher elevations on soils with comparatively higher proportions of silt and sand and with lower salinity levels, mostly on the West side of the plain.

Looking only at species-based dissimilarities, without considering trait data, the first eigenvalue of the PCoA is about twice as large as the second eigenvalue (Fig. 3B). In that case, the sites were roughly divided into two groups: those in the central part of the plain and those on the East and West side (Fig. 4A). Compared to the smoother gradient obtained with trait data, this pattern is more sensitive to changes in the elevation of the study area and less to the salinity gradient.

We finally compared the plot-to-plot dissimilarities obtained solely from species abundances with the corresponding functional dissimilarities. As expected, relaxing the constraint that all species are equally and maximally distinct from one another, trait-based dissimilarities were always lower than species-based dissimilarities (Fig. 4B). The functional dissimilarities among sites with no species in common (species-based dissimilarity = 1) varied between about 0 and 0.5 (Fig. 4B).

5. Discussion

Ecological data are often multivariate of high dimensionality. Therefore, no single measure adequately summarizes all aspects of (functional) dissimilarity among plots. In order to assess differences in the functional organization of species assemblages, a multifaceted approach is needed. In this paper, we thus proposed a new method for adapting traditional dissimilarity coefficients to the measurement of functional differences among plots. The resulting measures generalize species dissimilarity to include functional information. As such, they allow plot-to-plot comparisons at different levels of ecological complexity (i.e. compositional vs. functional dissimilarity), while avoiding confounding effects which may be due to differences in the calculation of the indices (Ricotta and Pavoine 2015).

The basic unit for the calculation of functional dissimilarity is the species ordinariness z_{uj} . In Appendix 3 we show that, in the special case where the species ordinariness are calculated from the relative abundances $p_{uj} = x_{uj} / \sum_{j=1}^N x_{uj}$ of each species, the resulting values of z_{uj} are tightly related to the notion of species rarity used by Patil and Taillie (1982) for providing a generalized definition of diversity measures. As such, our proposal may provide a starting point for developing a unified framework for the summarization of functional diversity and dissimilarity.

Note that species ordinariness was already used by Ricotta et al. (2015) for developing a single Bray and Curtis-like index of functional dissimilarity and by Ricotta and Pavoine (2015) for

288 constructing a family of functional dissimilarity measures based on a generalization of the classical
289 2×2 contingency table to include species abundances and interspecies resemblances. However,
290 these measures do not conform to the newly proposed branching requirement for functional
291 dissimilarity coefficients.

292 Given two assemblages U and V , the major difference between classical species abundance
293 values x_{Uj} and the corresponding species ordinariness z_{Uj} is that the former are stand-alone
294 quantities, which are independent of the abundances of the other species in U and V , whereas the
295 ordinariness of species j in plot U depends not only on its abundance x_{Uj} , but also on its functional
296 resemblance with the other species in U and V . Hence, using species ordinariness for the calculation
297 of plot-to-plot functional dissimilarity, we implicitly assume that species with similar traits are
298 likely to support similar functions, such that the selection of the most appropriate traits needs to be
299 explicitly targeted on the ecological process of interest. Also, although the formulation of species
300 uniqueness does not consider within-species differentiation, it is commonly agreed that species
301 differences in trait values are related to different mechanisms of resource use, such that the higher
302 the species overlap in functional space, the higher the species are expected to support similar
303 functions. Therefore, using dissimilarity measures based on functional overlap among species (Lepš
304 et al. 2006; Blonder et al. 2014), will allow us to include within-species differentiation in the
305 calculation of plot-to-plot functional dissimilarity.

306 To conclude, we hope our proposal will prove fruitful for summarizing plot-to-plot functional
307 dissimilarity in a meaningful way and for getting insights into the complex ecological mechanisms
308 that drive community structure.

309

310 **Supporting Information**

311 **Appendix 1.** Definitions and Proofs

312 **Appendix 2.** R scripts

313 **Appendix 3.** On the relationship between species ordinariness and species rarity

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368
369 **Figure 1.** Environmental patterns in the coastal marsh plain of La Mafragh. The locations of the
370 squares correspond to the geographic positions of the sample plots. The square size provides the
371 level of the environmental variables.
372

Figure 2. Results of the principal coordinate analysis applied to plot-to-plot functional dissimilarities after Cailliez transformation. (A) first axis of the PCoA applied to plot-to-plot functional dissimilarities. (B) Bar plot of the Spearman correlations between the first axis of the PcoA and the environmental variables.

Figure 3. Eigenvalue bar plot of the principal coordinate analysis applied to (A) plot-to-plot functional dissimilarities and (B) plot-to-plot species-based dissimilarities, after Cailliez transformation.

Figure 4. Species-based dissimilarities among plant communities in the coastal marsh plain of La Mafragh. (A) First axis of the principal coordinate analysis applied to species-based dissimilarities among plots. (B) Relationship between functional and species-based dissimilarities among plots. The dashed line corresponds to the theoretical scenario where species-based and functional dissimilarities would have equal values.

Appendix 1. Definitions and Proofs

Hereafter, we consider two plots U and V , where x_{Uj} and x_{Vj} are the abundance values of species j in plots U and V , respectively, N is the number of species of the pooled pair of plots (i.e. all species with non-zero abundance in at least one plot), and σ_{ij} is a symmetric similarity coefficient between species i and j bounded in the range $[0,1]$ with $\sigma_{ij} = \sigma_{ji}$ and $\sigma_{ii} = 0$.

Two species i and j will be said functionally identical if their functional similarity is maximal: $\sigma_{ij} = 1$.

Two plots U and V with no shared species are said functionally identical if for any species j (or any set of functionally identical species $j, j', j'', \dots$) in plot U , a species k (or a set of functionally identical species $k, k', k'', \dots$) exist in plot V such that $x_{Uj} = x_{Vk}$ and $\sigma_{jk} = 1$ (or $x_{Uj} + x_{Uj'} + x_{Uj''} + \dots = x_{Vk} + x_{Vk'} + x_{Vk''} + \dots$ and $\sigma_{jk} = 1$, in case of functionally identical species in U and/or in V), and if similarly for any species k (or a set of functionally identical species $k, k', k'', \dots$) in plot V , a species j (or any set of functionally identical species $j, j', j'', \dots$) exist in plot U such that $x_{Uj} = x_{Vk}$ and $\sigma_{jk} = 1$ (or $x_{Uj} + x_{Uj'} + x_{Uj''} + \dots = x_{Vk} + x_{Vk'} + x_{Vk''} + \dots$ and $\sigma_{jk} = 1$, in case of functionally identical species in U and/or in V).

1. For two identical plots U and V , the ordinariness z_{Uj} of species j in plot U is equal to the ordinariness z_{Vj} of species j in plot V .

For two identical plots, $x_{Uj} = x_{Vj}$ for all N species in U and V . Therefore, since $z_{Uj} = \sum_{i=1}^N x_{Ui} \sigma_{ij}$ (see Eq. 11 in the main text):

$$z_{Uj} = \sum_{i=1}^N x_{Ui} \sigma_{ij} = \sum_{i=1}^N x_{Vi} \sigma_{ij} = z_{Vj} \quad (\text{A1})$$

2. For two functionally identical plots U and V with no shared species, the ordinariness of species j in plot U is equal to the ordinariness of species j in plot V .

Consider the simplest case where U does not contain functionally identical species such that for all i and j in U , $\sigma_{ij} < 1$, and similarly V does not contain functionally identical species such that for all m and n in V , $\sigma_{mn} < 1$. In that case, functionally identical plots necessarily have the same number of species. In addition, for each pair of species i and j in U , we have a functionally identical pair of species m and n in V such that $x_{Ui} = x_{Vm}$, $\sigma_{im} = 1$, $x_{Uj} = x_{Vn}$, $\sigma_{jn} = 1$ and for all k in U and in V , $\sigma_{ik} = \sigma_{mk}$ and $\sigma_{kj} = \sigma_{kn}$. Therefore, we have:

$$z_{Uj} = \sum_{i \in U} x_{Ui} \sigma_{ij} \quad (\text{A2})$$

and

$$z_{Vj} = z_{Vn} = \sum_{m \in V} x_{Vm} \sigma_{mn} = \sum_{i \in U} x_{Ui} \sigma_{in} = \sum_{i \in U} x_{Ui} \sigma_{ij} = z_{Uj} \quad (\text{A3})$$

The demonstration for the more general case (where some species are allowed to be functionally identical within U and/or within V) can simply be obtained by pooling a set of functionally identical species within a plot into a single super-species with its abundance equal to the summed abundance of the functionally identical species. Indeed, the ordinariness values of functionally identical species in a plot are equal to each other, and are also equal to the ordinariness of the super-species (see proof at point 4 below, Eq. A8 and A9). For example, let $J = \{j, j', j'', \dots\}$ be such a super-species in U , such that $x_{UJ} = x_{Uj} + x_{Uj'} + x_{Uj''} + \dots$. If U and V are functionally identical, then there exist a species or a set of functionally identical species K in V such that $x_{UJ} = x_{VK}$ and $\sigma_{JK} = 1$.

3. For two maximally distinct plots with no species in common and with $\sigma_{jm} = 0$ for species j belonging to plot U and species m to plot V , z_{Vj} is always equal to zero, meaning that the species in U do not have any functional analogue in V , and z_{Um} is always equal to zero, meaning that the species in V do not have any functional analogue in U

Observing that

$$z_{Vj} = \sum_{m \in V} x_{Vm} \sigma_{jm} \quad (\text{A4})$$

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and

$$z_{Um} = \sum_{j \in U} x_{Uj} \sigma_{jm} \quad (\text{A5})$$

Since $\sigma_{jm} = 0$ by definition, we have $z_{Vj} = z_{Um} = 0$.

4. The general family of functional dissimilarity measures $D_w = \sum_{j=1}^N w_j d(z_{Uj}, z_{Vj})$, with $w_j = (x_{Uj} + x_{Vj}) / \sum_{k=1}^N (x_{Uk} + x_{Vk})$ (see Eq. 5 and 12 in the main text) conforms to the following branching requirement: the value of functional dissimilarity D_w among a pair of plots U and V does not change if a given species j is replaced by two functionally identical species with the same total abundance of j in U and V .

If species j is split into two species j' and j'' which are functionally identical to j such that $x_{Uj'} + x_{Uj''} = x_{Uj}$, $x_{Vj'} + x_{Vj''} = x_{Vj}$. Because j , j' and j'' are functionally identical $\sigma_{jj'} = \sigma_{jj''} = \sigma_{j'j''} = 1$, and for any species i in U and/or V , $\sigma_{ij} = \sigma_{ij'} = \sigma_{ij''}$. In addition, we have:

$$w_{j'} + w_{j''} = w_j \quad (\text{A6})$$

and

$$z_{Uj} = \sum_i x_{Ui} \sigma_{ij} = \sum_i x_{Ui} \sigma_{ij'} = \sum_i x_{Ui} \sigma_{ij''} \quad (\text{A7})$$

It follows that

$$z_{Uj'} = z_{Uj''} = z_{Uj} \quad (\text{A8})$$

and similarly

$$z_{Vj'} = z_{Vj''} = z_{Vj} \quad (\text{A9})$$

This yields

$$d(z_{Uj'}, z_{Vj'}) = d(z_{Uj''}, z_{Vj''}) = d(z_{Uj}, z_{Vj}) \quad (\text{A10})$$

Therefore, since $d(z_{Uj'}, z_{Vj'}) w_{j'} + d(z_{Uj''}, z_{Vj''}) w_{j''} = d(z_{Uj}, z_{Vj}) w_j$, it follows that D_w does not change if a given species j is split into two functionally identical species.

Appendix 2. R scripts

The R function “generalized_Traddiss” calculates plot-to-plot dissimilarity taking account of functional dissimilarities between species. This program is free software: you can redistribute it

500 and/or modify it under the terms of the GNU General Public License <http://www.gnu.org/licenses/>.
501 It will be integrated in a version of the adiv package after the publication of the associated paper.

502

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

506

507 **Description:** given a matrix of S species' relative or absolute abundance values $\times N$ plots, together
508 with an $S \times S$ (functional) dissimilarity matrix, the function "generalized_Traddidiss" calculates a
509 semimatrix with the values of the dissimilarity index for each pair of plots, as proposed in the main
510 text.

511

512 **Dependencies:** none.

513

514 **Usage:**

515 `generalized_Traddidiss <-`
516 `function(comm, dis, method = c("GC", "MS", "PE"), abundance = c("relative", "absolute", "none"),`
517 `weights = c("uneven", "even"), tol = 1e-8)`

518

519 **Arguments:**

520 *comm*: a matrix of N plots $\times S$ species containing the relative or absolute abundance of all species.
521 Columns are species and plots are rows. Column labels (species names) should be assigned as in the
522 *dis* matrix.

523

524 *dis*: an $S \times S$ matrix of dissimilarities between species rescaled in the range [0, 1] or an object of
525 class "dist" [obtained by functions like `vegdist` in package *vegan* (Oksanen *et al.* 2013), `gowdis` in
526 package *FD* (Laliberté & Shipley 2011), or `dist.ktab` in package *ade4* for functional dissimilarities
527 (Dray *et al.* 2007), or functions like `cophenetic.phylo` in package *ape* (Paradis *et al.* 2004) or
528 `distTips` in package *adephylo* (Jombart and Dray 2010) for phylogenetic dissimilarities]. If the
529 dissimilarities are outside the range 0-1, a warning message is displayed and each dissimilarity is
530 divided by the maximum over all pair-wise dissimilarities.

531

532 *method*: a character string giving the name of the coefficient of plot-to-plot dissimilarity to be
533 applied to species ordinariness (Z vectors defined in the main text, Eq. 11). It can be "GC", "MS",
534 or "PE". See details.

535

536 *abundance*: a character string with three possible values: "relative" for the use of relative species
537 abundance, "absolute" for the use of absolute species abundance, and "none" for the use of
538 presence/absence data (1/0).

539

540 *weights*: Two types of weights are available in the function: "uneven" (Eq. 5 in the main text) or
541 "even" ($1/S$, where S is the number of species in the two compared plots)

542

543 *tol*: a numeric tolerance threshold: a value between -tol and tol is considered as null.

544

545 **Details:**

546 The plot-to-plot dissimilarity coefficients used in this function are those listed in the main text.

547 Codes are as follows:

548 "GC": Equation 6 in the main text

549 "MS": Equation 8 in the main text

550 "PE": Equations 9 and 10 in the main text

551

552 **Value:**

553 The function returns a semi-matrix of class "dist" with the values of the proposed dissimilarities for

554 each pair of plots.

555

556 **Function Syntax**

```

557 generalized_Tradidiss <-
558 function(comm, dis, method = c("GC", "MS", "PE"), abundance = c("relative", "absolute",
559 "none"), weights = c("uneven", "even"), tol = 1e-8)
560 {
561   if(inherits(dis, "dist")) dis <- as.matrix(dis)
562   if(any(dis>1)){
563     warning("Phylogenetic dissimilarities are not in the range 0-1. They have been
564 normalized by the maximum")
565     dis <- dis/max(dis)
566   }
567   if(any(!colnames(comm) %in%rownames(dis))) stop("At least one species in the matrix
568 of abundances is missing in the matrix of dissimilarities")
569   if(any(!colnames(comm) %in%colnames(dis))) stop("At least one species in the matrix
570 of abundances is missing in the matrix of dissimilarities")
571   method <- method[1]
572   if(!method%in%c("GC", "MS", "PE")) stop("Incorrect definition for method")
573   abundance <- abundance[1]
574   if(!abundance%in%c("relative", "absolute", "none"))
575 stop("Incorrect definition for abundance")
576   weights <- weights[1]
577   if(!weights%in%c("uneven", "even")) stop("Incorrect definition for weights")
578   dis <- dis[colnames(comm), colnames(comm)]
579   dataset <- t(comm)
580   similarities <- 1-as.matrix(dis)
581   total <- colSums(dataset)
582   if(abundance == "relative")
583     abu <- sweep(dataset, 2, total, "/")
584   else if(abundance == "none"){
585     abu <- dataset
586     abu[abu>tol] <- 1
587     abu[abu<=tol] <- 0
588   }
589   else abu <- dataset
590   num.plot<-dim(dataset)[2]
591   num.sp <- dim(dataset)[1]
592   names<-list(colnames(dataset), colnames(dataset))
593   dis.matrix<-matrix(0, nrow=num.plot, ncol=num.plot, dimnames=names)
594   for (i in 2:num.plot) {
595     for (j in 1:(i-1)) {
596       mat_folk <- similarities*abu[, j]
597       mat_folk2 <- similarities*abu[, i]
598       Zik <- colSums(mat_folk)
599       Zih <- colSums(mat_folk2)
600       tabZ <- rbind.data.frame(Zik, Zih)
601       garde <- apply(tabZ, 2, sum)>tol & apply(abu[,c(i,j)], 1, sum)>tol
602       Zik <- Zik[garde]
603       Zih <- Zih[garde]
604       tabZ <- tabZ[, garde]
605       if(weights == "even") wk <- rep(1/length(Zih), length(Zih))
606       else {
607         wk <- (abu[, j]+abu[, i])/sum(abu[, c(i,j)])
608         wk <- wk[garde]
609       }

```

```

610     if(method == "CG") index <- sum((wk*abs(Zik-Zih)/apply(tabZ, 2, sum)))
611     else if(method == "MS") index <- sum((wk*abs(Zik-Zih)/apply(tabZ, 2, max)))
612     else {
613         zik <- Zik / (Zik + Zih)
614         zih <- Zih / (Zik + Zih)
615         tabz <- rbind.data.frame(zik, zih)
616         enlev <- as.vector(apply(tabz, 2,
617             function(x) any(x<=tol)))
618         zik <- zik[!enlev]
619         zih <- zih[!enlev]
620         wkN <- wk[!enlev]
621         wkY <- wk[enlev]
622         index <- sum(wkY) + sum(wkN*(1
623             +(zik * log(zik, base = 2)
624             + zih * log(zih, base = 2))))
625     }
626     dis.matrix[i, j] <- index
627 }
628 }
629 dis.matrix <- dis.matrix + t(dis.matrix)
630 dis.matrix <- dis.matrix + diag(rep(0, num.plot))
631 return(as.dist(dis.matrix))
632 }

```

633

634

635 Case study

636 Loading of package ade4 of R:

```
637 library(ade4)
```

638

639 Loading of the data set:

```
640 data(mafragh)
```

641

642 Species names:

```
643 namspe <- rownames(mafragh$traits[[1]])
```

644

645 Matrix with the abundance of plant species (columns) in plots (rows):

```
646 M <- mafragh$flo
```

```
647 colnames(M) <- namspe
```

648

649 Calculation of the functional dissimilarities between species (bounded between 0 and 1):

```
650 Bin <- prep.binary(mafragh$traits$tabBinary, c(3, 4))
```

```
651 distraits <- dist.ktab(ktab.list.df(list(mafragh$traits$tabOrdinal[,2:3], Bin)),
652 c("O","B"), scan=TRUE)
```

653 Choose your metric for binary variables

654 1 = JACCARD index (1901) S3 coefficient of GOWER &

655 LEGENDRE

```
656 s1 = a/(a+b+c) --> d = sqrt(1 - s)
```

657 2 = SOCKAL & MICHENER index (1958) S4 coefficient of GOWER & LEGENDRE

```
658 s2 = (a+d)/(a+b+c+d) --> d = sqrt(1 - s)
```

659 3 = SOCKAL & SNEATH(1963) S5 coefficient of GOWER &

660 LEGENDRE

```
661 s3 = a/(a+2(b+c)) --> d = sqrt(1 - s)
```

662 4 = ROGERS & TANIMOTO (1960) S6 coefficient of GOWER &

663 LEGENDRE

```
664 s4 = (a+d)/(a+2(b+c)+d) --> d = sqrt(1 - s)
```

665 5 = CZEKANOWSKI (1913) or SORENSEN (1948) S7 coefficient of GOWER & LEGENDRE

```
666 s5 = 2*a/(2*a+b+c) --> d = sqrt(1 - s)
```

667 6 = S9 index of GOWER & LEGENDRE (1986)

```
668 s6 = (a-(b+c)+d)/(a+b+c+d) --> d = sqrt(1 - s)
```

669 7 = OCHIAI (1957) S12 coefficient of GOWER & LEGENDRE

```
670 s7 = a/sqrt((a+b)(a+c)) --> d = sqrt(1 - s)
```

671 8 = SOKAL & SNEATH (1963) S13 coefficient of GOWER &

672 LEGENDRE

```

673 s8 = ad/sqrt((a+b) (a+c) (d+b) (d+c)) --> d = sqrt(1 - s)
674 9 = Phi of PEARSON = S14 coefficient of GOWER & LEGENDRE
675 s9 = (ad-bc)/sqrt((a+b) (a+c) (b+d) (d+c)) --> d = sqrt(1 -
676 s)
677 10 = S2 coefficient of GOWER & LEGENDRE
678 s10 = a/(a+b+c+d) --> d = sqrt(1 - s) and unit
679 self-similarity
680 Select an integer (1-10): 5
681 Choose your metric for ordinal variables
682 1 = ranked variables treated as quantitative variables
683 2 = Podani (1999)'s formula
684 Select an integer (1-2): 1
685 Choose your metric for quantitative variables
686 1 = Euclidean
687 d1 = Sum((x(i)-y(i))^2)/n
688 2 = Manhattan
689 d2= Sum(|x(i)-y(i)|)/n
690 Select an integer (1-2): 1
691
692 Application of the Bray-Curtis index (Eq. 4 of the main text) or equivalently index GC (Eq. 6) with
693 uneven weights for species (Eq. 5) to the data set:
694 disGC <- generalized_Tradidiss(M, distraits, method="GC")
695
696 The functional dissimilarities between plots do not have the Euclidean properties
697 is.euclid(as.dist(disGC))
698 [1] FALSE
699
700
701 First approach: Principal coordinate analysis (PCoA) on the functional dissimilarities transformed
702 by Cailliez approach (addition to the dissimilarities of the smallest constant that renders the
703 dissimilarities Euclidean)
704 pcoGC <- dudi.pco(as.dist(cailliez(disGC)))
705 Select the number of axes: 2
706
707 Coordinates of the species on the first axis of the PCoA (given by the color and size of a square) at
708 their spatial location in the plain La Mafragh (a square is at the geographic position of its associated
709 plot):
710 s.value(mafragh$xy, pcoGC$li[,1])
711

```

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Second approach: non-metric Multidimensional Scaling analysis (nMDS) on the functional dissimilarities

```
CMD <- cmdscale(disGC)
summary(CMD)
```

	V1	V2
Min.	:-0.258573	Min. :-0.077484
1st Qu.:	-0.060668	1st Qu.:-0.014220
Median :	0.005213	Median :-0.001209
Mean :	0.000000	Mean : 0.000000
3rd Qu.:	0.053966	3rd Qu.: 0.010996
Max. :	0.291525	Max. : 0.099926

The coordinates on the second axis of the nMDS are low indicating that most of the functional variation between plots is expressed by the first axis.

Spatial pattern of the first axis of the nMDS:

```

733 s.value(mafragh$xy, CMD[,1])
734

```

```

735
736
737
738 Link between the coordinates of plots in PCoA and those in the nMDS:

```

```

739
740 plot(pcoGC$li[,1], CMD[,1], xlab="First axis of PCoA", ylab="First axis of
741 nMDS")

```

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743
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746

Analysis of the species-based dissimilarities between plots:

747 Species are defined as maximally dissimilar:
748 `DM1 <- as.dist(matrix(1, 56,56))`
749 `attributes(DM1)$Labels <- attributes(distrails)$Labels`
750

751 Application of the Bray-Curtis index (Eq. 4 of the main text) or equivalently index GC (Eq. 6) with
752 uneven weights for species (Eq. 5) to the data set with species defined as maximally dissimilar:
753 `disM1 <- generalized_Traddidiss(M, DM1)`
754

755 The species-based dissimilarities between plots do not have the Euclidean properties
756 `is.euclid(disM1)`
757 `[1] FALSE`
758

759 Principal Coordinate Analysis of the species-based dissimilarities between plots

760 `pcoDM1 <- dudi.pco(as.dist(cailliez(disM1)))`
761 `Select the number of axes: 2`
762


```
763 Eigenvalue bar plot:  
764 barplot(pcoDM1$eig)
```

```
765  
766  
767 Coordinates of the species on the first axis of the PCoA (given by the color and size of a square) at  
768 their spatial location in the plain La Mafragh (a square is at the geographic position of its associated  
769 plot):  
770 s.value(mafragh$xy, pcoDM1$li[,1], csize=0.5)
```

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779

Link between the species-based and the functional dissimilarities between plots:

```
plot(disM1, disGC, asp=1, ylim=c(0,1), xlab="species-based dissimilarities
between plots", ylab="functional dissimilarities between plots")
lines(c(0,1), c(0,1))
```

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Analysis of environmental data on the factorial map of the functional PCoA:

Environmental data:

```
env <- mafragh$env[-(8:10)]
```

788 Correlations between environmental data and the coordinates of plots on the first axis of the
789 functional PCoA:

```
790 cor(env, pcoGC$li[,1], method="spearman")
791           [,1]
792 Clay      -0.3441044
793 Silt       0.2214038
794 Sand       0.4734112
795 K2O       -0.3989277
796 Mg++      -0.2372428
797 Na+/100g  -0.5128574
798 K+        -0.6414609
799 Elevation  0.3561348
```

```

800
801 barplot(cor(env, pcoGC$li[,1], method="spearman"))

```

```

802
803

```

```

804
805

```

References

- ```

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```

```

818
819

```

### Appendix 3. On the relationship between species ordinariness and species rarity

```

820
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822

```

```

823 Let U and V be two plots (or communities, assemblages, relevés, sites, quadrats, etc.) where x_{Uj} and
824 x_{Vj} are the abundance values of species j in plots U and V , respectively, $p_{Uj} = x_{Uj} / \sum_{j=1}^N x_{Uj}$ is the
825 relative abundance of species j in plot U (with $0 \leq p_{Uj} \leq 1$ and $\sum_{j=1}^N p_{Uj} = 1$), and N is the total
826 number of species sampled in both plots (i.e. the species for which $\min\{x_{Uj}, x_{Vj}\} > 0$). Leinster and
827 Cobbold (2012) defined the ordinariness of species j in plot U as:

```

$$z_{Uj} = \sum_{i=1}^N x_{Ui} \sigma_{ij} \quad (\text{A1})$$

where  $z_{Uj}$  is the abundance of all species that are functionally similar to  $j$  (including  $j$  itself), and  $\sigma_{ij}$  is a symmetric similarity coefficient between species  $i$  and  $j$  such that  $\sigma_{ij} = \sigma_{ji}$  and  $\sigma_{jj} = 0$ . For species  $j$ ,  $z_{Uj}$  thus measures the commonness of all individuals in plot  $U$  that support the functions associated with  $j$ .

In the main text, we showed that the quantity  $z_{Uj}$  can be used for deriving a general family of functional dissimilarity coefficients among plots  $U$  and  $V$  (see Eq. 10 of the main text). Here, we show that if species ordinariness  $z_{Uj}$  is calculated from the species relative abundances  $p_{Uj}$  such that

$$z_{Uj} = \sum_{i=1}^N p_{Ui} \sigma_{ij} \quad (\text{A2})$$

the resulting measure is tightly related to the notion of species rarity used by Patil and Taillie (1982) for providing a general definition of diversity coefficients.

Rao (1982) introduced a diversity index, termed Quadratic diversity, for summarizing mean interspecies differences within a given plot. The quadratic diversity of plot  $U$  is defined as the expected dissimilarity between two individuals drawn randomly with replacement from the plot:

$$Q_U = \sum_{j=1}^N \sum_{i=1}^N p_{Ui} p_{Uj} \delta_{ij} \quad (\text{A3})$$

where  $\delta_{ij}$  is the dissimilarity among species  $i$  and  $j$ .

For a review of some relevant mathematical properties of Rao's  $Q$  see Pavoine (2012). Here, it is sufficient to observe that if  $\delta_{ij}$  is bounded between 0 and 1, assuming that all species are maximally distinct from one another (i.e. if  $\delta_{ij} = 1$  for all  $i \neq j$ ),  $Q_U$  reduces to the classical Simpson index of diversity  $S_U = 1 - \sum_{j=1}^N p_{Uj}^2$ . Also, because  $0 \leq \delta_{ij} \leq 1$ , an associated measure of concentration or dominance (i.e. the opposite of diversity) can be defined as the complement of Rao's  $Q$  (Leinster and Cobbold 2012):

$$D_U = 1 - Q_U = \sum_{j=1}^N \sum_{i=1}^N p_{Ui} p_{Uj} \sigma_{ij} \quad (\text{A4})$$

where  $D_U$  is the average similarity between all species in plot  $U$ , and  $\sigma_{ij} = 1 - \delta_{ij}$ .

To gain insight into the type of diversity measured by the Simpson and the Rao coefficients, it is convenient to express Simpson in the form  $S_U = \sum_{j=1}^N p_{Uj} (1 - p_{Uj})$ . In the context of interspecific encounter theory, Patil and Taillie (1982) defined the Simpson diversity as the probability that two individuals drawn randomly from a given plot do not belong to the same species. Therefore, the Simpson diversity is essentially a measure of uncertainty in predicting the relative abundance of the species in the plot. In information theory and statistics, the quantity  $(1 - p_{Uj})$  is usually referred to as the surprise or rarity associated to species  $j$  (Ricotta and Szeidl 2006; Leinster and Cobbold 2012). If  $p_{Uj}$  is small, we would be quite surprised in finding species  $j$ . To the contrary, if  $p_{Uj}$  is

large, the surprise in finding  $j$  is small. Patil and Taillie (1982) thus proposed a general definition of diversity ( $\Delta$ ) as the average rarity  $\rho(p_{Uj})$  of a given assemblage

$$\Delta = \sum_{j=1}^N p_{Uj} \rho(p_{Uj}) \quad (\text{A5})$$

where  $\rho(p_{Uj})$  is some decreasing function of the species relative abundance  $p_{Uj}$ .

Klir and Wierman (1999) and Ricotta and Szeidl (2006) noted that the quantity  $(1 - p_{Uj}) = \sum_{i \neq j} p_{Ui}$  measures the relative abundance of all species that differ from species  $j$ . That is, the probabilities of all events that conflict with  $p_{Uj}$ . Accordingly, assuming that all species are maximally distinct from each other (i.e. if  $\delta_{ij} = 1$  for all  $i \neq j$ ), the Simpson index can be interpreted as a measure of the expected conflict  $C(p_{Uj})$  of all species in the assemblage (Ricotta and Szeidl 2006):

$$S_U = \sum_{j=1}^N p_{Uj} \sum_{i \neq j} p_{Ui} = \sum_{j=1}^N p_{Uj} C(p_{Uj}) \quad (\text{A6})$$

Relaxing the constraint of maximal dissimilarity among species, it seems natural to summarize the conflict of species  $j$  with the other species in the assemblage taking into account their pairwise distances  $\delta_{ij}$  such that:

$$C(p_{Uj}) = \sum_{i=1}^N p_{Ui} \delta_{ij} \quad (\text{A7})$$

with  $\delta_{jj} = 0$ . Accordingly, incorporating a measure of pairwise dissimilarity among species, the Simpson expression of expected conflict becomes Rao's quadratic diversity  $\sum_{j=1}^N p_{Uj} \sum_{i=1}^N p_{Ui} \delta_{ij}$ . Rao's  $Q$  can be thus interpreted as a general measure of expected rarity or conflict in a given assemblage if the species are not treated as maximally distinct from each other (Ricotta and Szeidl 2006).

Likewise, we can define the ordinariness of species  $j$  as the complement of its conflict:

$$z_{Uj} = 1 - C(p_{Uj}) = \sum_{i=1}^N p_{Ui} \sigma_{ij} \quad (\text{A8})$$

such that the expected species concentration in Eq. A4 can be rewritten as  $D_U = \sum_{j=1}^N p_{Uj} \sum_{i=1}^N p_{Ui} \sigma_{ij} = \sum_{j=1}^N p_{Uj} z_{Uj}$ , while Rao's diversity becomes  $Q_U = 1 - \sum_{j=1}^N p_{Uj} z_{Uj}$ , where the ordinariness  $z_{Uj}$  is the expected similarity between an individual of species  $j$  and an individual drawn randomly from the assemblage.

Therefore, according to the above derivation, if the values of  $z_{Uj}$  are calculated from the species relative abundances  $p_{Uj}$ , species ordinariness may represent a common currency for expressing both the species functional diversity in single plots and their functional dissimilarity among pair of plots.

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