Methods in Ecology and Evolution

British Ecological Society

Methods in Ecology and Evolution 2014, **5,** 666–675 doi: 10.1111/2041-210X.12193

Functional and phylogenetic similarity among communities

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Summary

1. Ecological studies often rely on coefficients of intercommunity (dis)similarity to decipher effects of ecological, evolutionary and human-driven mechanisms on the composition of communities. Yet, two main criticisms have been levelled at (dis)similarity coefficients. First, few developments include information on species' abundances, and either phylogeny or functional traits. Secondly, some (dis)similarity coefficients fail to always provide maximum dissimilarity between two completely distinct communities, that is, communities without common species and with zero similarities among their species.

2. Here, we introduce a new family of similarity coefficients responding to these criticisms. Within this family, we concentrate on four coefficients and compare them to Rao's dissimilarity on macroinvertebrate communities, and simulated data.

3. Our new coefficients correctly treat maximally dissimilar communities: similarities are always zero between two completely distinct communities. The originality of these new coefficients is even more profound as the existence of maximally dissimilar communities was not a requirement for the new coefficients to behave differently than Rao's dissimilarity coefficient.

4. Our new family of similarity coefficients relies on the abundances or occurrences of species within communities and on phylogenetic, taxonomic or functional similarities among species. We demonstrate that this new family embeds many of the recent developments in both functional and phylogenetic diversity. It provides a unique framework for comparing traditional compositional turnover with functional or phylogenetic similarities among communities.

Key-words: beta diversity, biodiversity, choice of coefficient, community ecology, community phylogenetics, compositional turnover, principle of maximum dissimilarity, quadratic entropy

Introduction

There are many different coefficients for expressing the (dis)similarity between two communities (or plots, stations, samples, assemblages, etc.). The large majority of these measures attempts to summarize different aspects of community-to-community dissimilarity based either on species presences and absences within communities or on species abundances. However, the utility of dissimilarity measures that incorporate information about the degree of ecological differences between the species in both communities is becoming increasingly recognized (Pavoine, Dufour & Chessel 2004; Lozupone & Knight 2005; Ferrier *et al.* 2007; Bryant *et al.* 2008; Graham & Fine 2008; Webb, Ackerly & Kembel 2008; Ricotta & Szeidl 2009; Ives & Helmus 2010; Nipperess, Faith & Barton 2010; Chiu, Jost & Chao 2014). Such interspecies differences can be based either on phylogenetic or on functional relationships among species, as ecological differences between species are believed to be reflected in both of them (Webb *et al.* 2002).

To summarize mean interspecies differences within single communities, Rao (1982) proposed a diversity index, termed quadratic diversity (Q), that is defined as the expected dissimilarity between two individuals of a given community randomly drawn with replacement:

$$Q = \sum_{ij} p_i p_j \delta_{ij} \qquad \text{eqn 1}$$

where p_i is the relative abundance of species i (i = 1, 2, . . ., N) with $p_i \geq 0$ and $\sum_i p_i = 1$, and $\mathbf{\Delta} = (\delta_{ij})$, where i, j = 1, 2, . . ., N, is a symmetric matrix of pairwise (functional or phylogenetic) dissimilarities among all species i and j. Given two

*Correspondence author. E-mail: pavoine@mnhn.fr communities with relative abundance vectors $\mathbf{p} = (p_1 \ldots p_i \ldots p_N)^t$ and $\mathbf{q} = (q_1 \ldots q_i \ldots q_N)^t$, where t is the transpose, Rao (1982) defined a dissimilarity coefficient:

$$D_Q = \sum_{ij} p_i q_j \delta_{ij} - \frac{1}{2}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{2}\sum_{ij} q_i q_j \delta_{ij} \qquad \text{eqn 2}$$

where $\sum_{ij} p_i q_j \delta_{ij}$ is the expected dissimilarity between two randomly drawn individuals, one from each community. D_Q is thus obtained by subtracting the mean of within-community diversities from among-community diversity. If $\mathbf{\Delta} = (\delta_{ij})$ is squared Euclidean (a mathematical property described in the Glossary in Table 1) and if $0 \leq \delta_{ij} \leq 1$, for all i and j, D_Q is bounded between 0 and 1 due to the concavity of function $Q(\mathbf{p}) = \sum_{ij} p_i p_j \delta_{ij}$ (i.e. $Q(\frac{\mathbf{p}+\mathbf{q}}{2}) \geq \frac{1}{2}Q(\mathbf{p}) + \frac{1}{2}Q(\mathbf{q})$, with $Q(\frac{\mathbf{p}+\mathbf{q}}{2})$ being Rao's quadratic entropy index computed from vector $(\mathbf{p} + \mathbf{q})/2$, Champely & Chessel 2002). Concavity here means that diversity increases by mixing so that the diversity in a pool of communities is always higher than (or equal to) the average diversity within the communities.

Referring to Jost's (2006) observations on more traditional dissimilarity indices, Ricotta and Szeidl (2009) observed that Rao's dissimilarity coefficient fails to always provide maximum dissimilarity between two completely distinct communities. If two communities are completely distinct, that is, if they have no species in common and $\delta_{ij} = 1$ for species i belonging to the first community and species j to the second one, we expect the average dissimilarity between the species of the first and the species of the second community, that is, $\sum_{ij} p_i q_j \delta_{ij}$, to be equal to unity. Yet, in that case, D_Q can be low if $\sum_{ij} p_i p_j \delta_{ij}$ or $\sum_{ij} q_i q_j \delta_{ij}$, which measure the diversity within each community, is high. The main objective of this study was thus to introduce new (dis)similarity coefficients that provide maximum dissimilarity (and thus zero similarity) between two completely distinct communities.

Methods

A NEW FAMILY OF SIMILARITY INDICES

A way of providing maximum dissimilarity between two completely distinct communities as recommended by Jost (2006) and Ricotta and Szeidl (2009) is to standardize the dissimilarity coefficient D_Q by dividing it by the value expected for two completely distinct theoretical communities with the same quadratic diversity as the real communities (see Meirmans 2006 for the use of a related standardization process in genetics). The standardized coefficient would thus be:

$$D_{st} = \frac{\sum_{ij} p_i q_j \delta_{ij} - \frac{1}{2}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{2}\sum_{ij} q_i q_j \delta_{ij}}{1 - \frac{1}{2}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{2}\sum_{ij} q_i q_j \delta_{ij}} \qquad \text{eqn 3}$$

Because D_{st} is bounded between 0 and 1, an associated similarity coefficient can be defined as $S_{st} = 1 - D_{st}$. Using interspecies similarities instead of dissimilarities, the expression of S_{st} simplifies to:

$$S_{st} = \frac{\sum_{ij} p_i q_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} p_i p_j \sigma_{ij} + \frac{1}{2}\sum_{ij} q_i q_j \sigma_{ij}} \qquad \text{eqn 4}$$

where $\sigma_{ij} = 1 - \delta_{ij}$ for all i, j is a measure of pairwise (functional or phylogenetic) similarity among species (Appendix S1, section 1.1). This paper will show that S_{st} is a special case of a more general formula, which contains well-known indices such as the Sørensen (1948) and Horn (1966) coefficients, together with more special cases.

The standardization of D_Q opens the way for constructing a new family of similarity coefficients. First, dealing with interspecies similarities σ_{ij}, the relative abundance vectors $\mathbf{p}$ and $\mathbf{q}$ can be replaced by more general vectors $\mathbf{x} = (x_1 \ldots x_i \ldots x_N)^t$ and $\mathbf{z} = (z_1 \ldots z_i \ldots z_N)^t$ where any nonnegative value is allowed (i.e. the quantities x_i and z_i are not necessarily required to sum to one). Vectors $\mathbf{x}$ and $\mathbf{z}$ can contain either presence/absence (1/0) scores, absolute abundance values, such as individual counts or biomass data, or relative abundance data that sum to one over all species in a given community. Next, several similarity indices (Table 2) can be developed by considering different combinations of the between-community component $\sum_{ij} x_i z_j \sigma_{ij}$ and the within-community components $\sum_{ij} x_i x_j \sigma_{ij}$ and $\sum_{ij} z_i z_j \sigma_{ij}$ (see Table 2). Among the many possible measures that have been developed for calculating community (dis)similarity (Podani 2000; Legendre & Legendre 2012), the index

$$S_{Sokal-Sneath} = \frac{\sum_{ij} x_i z_j \sigma_{ij}}{2\sum_{ij} x_i x_j \sigma_{ij} + 2\sum_{ij} z_i z_j \sigma_{ij} - 3\sum_{ij} x_i z_j \sigma_{ij}} \qquad (5)$$

is a generalization of an index proposed by Sokal and Sneath (1963) for the presence/absence scores. Indeed, using species presence/absence data and setting $\sigma_{ij} = 0$ for $i \neq j$ and $\sigma_{ii} = 1$, then $\sum_{ij} x_i z_i \sigma_{ij} = a$ is the number of species shared by the two communities, $\sum_{ij} x_i x_j \sigma_{ij} = a + b$ is the total number of species in the first community (with b the number of species in the first community that are absent from the second community), and $\sum_{ij} z_i z_j \sigma_{ij} = a + c$ is the total number of species in the second community (with c the number of species in the second com-

Table 1. Glossary

	Definition
Dissimilarity	Here dissimilarity between two entities i and j (e.g. two species or two communities) denotes any nonnegative value d_{ij} that measures any functional or phylogenetic difference between the two entities, with $d_{ii} = 0$. In this paper, the discussion is limited to symmetric dissimilarities bounded between 0 and 1
Similarity	In this paper, the discussion is limited to symmetric similarities bounded between 0 and 1 so that $s_{ij} = 1 - d_{ij}$ for all i and j
Distance matrix	A matrix of dissimilarities $\mathbf{D} = (d_{ij})$, for all $i, j = 1, \ldots, N$ is a distance matrix if $d_{ij} \leq d_{ik} + d_{kj}$ for all $i, j, k = 1, \ldots, N$
Euclidean matrix	A matrix of dissimilarities $\mathbf{D} = (d_{ij})$, for all $i, j = 1, \ldots, N$, is Euclidean if one can find N points $M_1, \ldots, M_N$ in a Euclidean space, so that the Euclidean distance between any two points M_i, M_j is d_{ij}. Euclidean matrices are distance matrices
Squared Euclidean matrix	A matrix of dissimilarities $\mathbf{D} = (d_{ij})$, for all $i, j = 1, \ldots, N$, is squared Euclidean if the matrix $\left(\sqrt{d_{ij}}\right)$, for all $i, j = 1, \ldots, N$, is Euclidean
Positive semi-definite matrix	Let $\mathbf{A}$ be a square matrix (a_{ij}), for all $i, j = 1, \ldots, N$. $\mathbf{A}$ is positive semi-definite (=non-negative definite) if, for any real vector $\mathbf{x} = (x_1 \ldots x_N)^t$, $\sum_{i=1}^{N}\sum_{j=1}^{N} x_i x_j a_{ij} \geq 0$

Table 2. Similarity indices

	General formula (**x, z** positive)*	Special cases: maximally distinct species[†]			
		x, z positive*	Reference[‡]	Presence/absence only[§]	Reference[‡]
$S_{Sokal\text{-}Sneath}$	$\frac{\sum_{ij} x_i z_j \sigma_{ij}}{2\sum_{ij} x_i x_j \sigma_{ij} + 2\sum_{ij} z_i z_j \sigma_{ij} - 3\sum_{ij} x_i z_j \sigma_{ij}}$	$\frac{\sum_i x_i z_i}{2\sum_i x_i^2 + 2\sum_i z_i^2 - 3\sum_i x_i z_i}$		$\frac{a}{a+2b+2c}$	Sokal & Sneath (1963)
$S_{Jaccard}$	$\frac{\sum_{ij} x_i z_j \sigma_{ij}}{\sum_{ij} x_i x_j \sigma_{ij} + \sum_{ij} z_i z_j \sigma_{ij} - \sum_{ij} x_i z_j \sigma_{ij}}$	$\frac{\sum_i x_i z_i}{\sum_i x_i^2 + \sum_i z_i^2 - \sum_i x_i z_i}$	Wishart (1969)	$\frac{a}{a+b+c}$	Jaccard (1901)
$S_{Sørensen}$	$\frac{\sum_{ij} x_i z_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} x_i x_j \sigma_{ij} + \frac{1}{2}\sum_{ij} z_i z_j \sigma_{ij}}$	$\frac{\sum_i x_i z_i}{\frac{1}{2}\sum_i x_i^2 + \frac{1}{2}\sum_i z_i^2}$	Morisita (1959) and Horn (1966)	$\frac{2a}{2a+b+c}$	Dice (1945) and Sørensen (1948)
S_{Ochiai}	$\frac{\sum_{ij} x_i z_j \sigma_{ij}}{\sqrt{\sum_{ij} x_i x_j \sigma_{ij}}\sqrt{\sum_{ij} z_i z_j \sigma_{ij}}}$	$\frac{\sum_i x_i z_i}{\sqrt{\sum_i x_i^2}\sqrt{\sum_i z_i^2}}$		$\frac{a}{\sqrt{a+b}\sqrt{a+c}}$	Ochiai (1957)

*$\mathbf{x} = (x_1 \ldots x_i \ldots x_N)^t$ and $\mathbf{z} = (z_1 \ldots z_i \ldots z_N)^t$ contain positive values attributed to N species within two communities: for example presence/absence (1/0), absolute values (e.g. abundance, biomass) or proportions that sum to 1 (e.g. relative abundance, relative biomass).

[†]Here $\sigma_{ij} = 0$ for all $i \neq j$ and $\sigma_{ii} = 1$. Species are thus all maximally different.

[‡]See Gleason (1920) in addition to Dice (1945) and Sørensen (1948). The formula $\sum_i x_i z_i / \sqrt{\sum_i x_i^2 \sum_i z_i^2}$ is related to the chord distance introduced in ecology by Orlóci (1967).

[§]a = number of species shared by the two communities; b = number of species found solely in the first community; and c = number of species found in the second community only.

munity that are absent from the first community). In this special case, the coefficient $S_{Sokal\text{-}Sneath}$ reduces to

$$\frac{a}{a+2b+2c} \qquad \text{eqn 6}$$

an index introduced by Sokal and Sneath (1963) as a measure of species turnover.

Likewise, the index

$$S_{Jaccard} = \frac{\sum_{ij} x_i z_j \sigma_{ij}}{\sum_{ij} x_i x_j \sigma_{ij} + \sum_{ij} z_i z_j \sigma_{ij} - \sum_{ij} x_i z_j \sigma_{ij}} \qquad \text{eqn 7}$$

turns out to be a generalization of the index developed by Jaccard (1901) for the presence/absence data and that of Wishart (1969) for species abundances (Table 2), while the index

$$S_{Sørensen} = \frac{\sum_{ij} x_i z_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} x_i x_j \sigma_{ij} + \frac{1}{2}\sum_{ij} z_i z_j \sigma_{ij}} \qquad \text{eqn 8}$$

is a generalization of the index S_{st} introduced above. $S_{Sørensen}$ is also a generalization of the Dice–Sørensen index for the presence/absence data and Morisita–Horn index for species abundances (Dice 1945; Sørensen 1948; Morisita 1959; Horn 1966; Table 2). When applied to ultrametric phylogenetic similarities among species, this index is related to the phylo-Morisita–Horn index of Chiu, Jost and Chao (2014; see Appendix S1, section 1.2). The index $S_{Sørensen}$ provides, however, more flexibility in the types of similarities among species that can be used. Finally, if, in the denominator of $S_{Sørensen}$, the arithmetic mean $\frac{1}{2}S_A + \frac{1}{2}S_B$ is replaced by the geometric mean $\sqrt{S_A}\sqrt{S_B}$, we obtain

$$S_{Ochiai} = \frac{\sum_{ij} x_i z_j \sigma_{ij}}{\sqrt{\sum_{ij} x_i x_j \sigma_{ij}}\sqrt{\sum_{ij} z_i z_j \sigma_{ij}}} \qquad \text{eqn 9}$$

which is an extension of the well-known index developed by Ochiai (1957) to incorporate interspecies measures of functional or phylogenetic similarity (see Table 2). S_{Ochiai} is also related to the chord distance introduced in ecological studies by Orlóci (1967; see also Burt 1948 and Tucker 1951).

All these indices are bounded between 0 and 1 (section 1.3 in Appendix S1) and lead to positive semi-definite (p.s.d.) matrices $\mathbf{S} = (s_{ij})$ of intercommunity similarities if the interspecies similarity matrix $\mathbf{\Sigma} = (\sigma_{ij})$ is also p.s.d. (see Glossary and Appendix S1 section 1.4). This property implies that the dissimilarity matrices $\mathbf{D} = \left(\sqrt{1-s_{ij}}\right)$ and $\Delta = \left(\sqrt{1-\sigma_{ij}}\right)$ are Euclidean so that they can be associated with clouds of points in Euclidean space (Gower & Legendre 1986; see Glossary).

The following inequalities exist among the new indices: $0 \leq S_{Sokal\text{-}Sneath} \leq SJaccard \leq S_{Sørensen} \leq S_{Ochiai} \leq 1$ (section 1.5 in Appendix S1). Some properties of the new indices depend on their extrema. When two communities are completely distinct with no species in common and $\sigma_{ij} = 0$ for species i occurring in the first community and species j in the second one, all indices in Table 2 equal zero. A difference among the new similarity coefficients is that coefficients $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$ and $S_{Sørensen}$ all equal 1 (perfect similarity) when $\sum_{ij} x_i z_j \sigma_{ij}$ equals $\frac{1}{2}\sum_{ij} x_i x_j \sigma_{ij} + \frac{1}{2}\sum_{ij} z_i z_j \sigma_{ij}$ (arithmetic mean), whereas S_{Ochiai} equals 1 when $\sum_{ij} x_i z_j \sigma_{ij}$ equals $\sqrt{\sum_{ij} x_i x_j \sigma_{ij}}\sqrt{\sum_{ij} z_i z_j \sigma_{ij}}$ (geometric mean). In both cases, perfect similarity includes the situation where $\mathbf{x} = \mathbf{z}$ but not exclusively. Perfect similarity is thus obtained wherever there is, on average, no more similarity among species within communities than between communities.

CONSTRAINTS FOR DEVELOPING THE NEW FAMILY OF SIMILARITY INDICES

When combining components $\sum_{ij} x_i z_j \sigma_{ij}$, $\sum_{ij} x_i x_j \sigma_{ij}$ and $\sum_{ij} z_i z_j \sigma_{ij}$, the first criterion is of course that the combination leads to a similarity index. Our second criterion was to restrict our family to relative similarity indices bounded between 0 and 1. Without this restriction, the component $\sum_{ij} x_i z_j \sigma_{ij}$ itself could be used as an index of similarity among communities. Indeed, in the same line, Webb, Ackerly and Kembel (2008) suggested the following formula, designated as COMDIST in the software Phylocom, for measuring the dissimilarity between two communities: $\sum_{ij} p_i q_j \delta_{ij}$, with p_i the relative abundance of species *i* in community A, q_j the relative abundance of species *j* in community B and δ_{ij} the phylogenetic dissimilarity between *i* and *j*. Like $\sum_{ij} x_i z_j \sigma_{ij}$, COMDIST is an absolute index that does not consider how diverse communities are. In the next sections, we illustrate with a simple theoretical data set, the consequences the use of COMDIST can have when measuring the dissimilarity between two communities. On the other hand, index standardization between 0 and 1, like for all indices of the new family, is not without consequences. For instance, one has first to fix a value (generally unity) for maximum similarity among species, such that interspecies similarities are bounded between 0 and this maximum. If the dissimilarities among species are multiplied by 2, the resulting values of COMDIST and D_Q are also multiplied by 2. Such multiplicity does not hold for similarity indices bounded between 0 and 1, like $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}. Also, if the similarity values among distinct species are divided by a constant (leaving the similarity between individuals of the same species equal to unity, i.e. $\sigma_{ii} = 1$), then the values of $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai} will depend on how this division modifies the index components $\sum_{ij} x_i z_j \sigma_{ij}$, $\sum_{ij} x_i x_j \sigma_{ij}$, and $\sum_{ij} z_i z_j \sigma_{ij}$, and how these components are combined in the formulation of the different indices. Altogether, the results obtained with any index applied to different data sets will be comparable only if the (dis)similarities among species have been defined in the same way (see Appendix S2 for a short discussion on the definition of taxonomic, phylogenetic and functional similarities among species).

Given the high number of possibilities to combine the three index components $\sum_{ij} x_i z_j \sigma_{ij}$, $\sum_{ij} x_i x_j \sigma_{ij}$, and $\sum_{ij} z_i z_j \sigma_{ij}$ into an index of similarity, we further restricted our discussion to indices that lead to p.s.d. similarity matrices. Although this property might not be critical for many ecological studies, it is an interesting property when (dis)similarities among communities have to be visualized graphically. Indeed, as mentioned above, when the matrix $\mathbf{S} = (s_{ij})$ of pairwise similarities among communities is p.s.d., then the associated dissimilarity matrix $\mathbf{D} = \left(\sqrt{1 - s_{ij}}\right)$ is Euclidean. Being Euclidean, the dissimilarities among communities can be associated with clouds of points using principal coordinate analysis (Gower & Legendre 1986). With this methodology, the cloud of points can be projected in a finite number of dimensions that best express how (functionally or phylogenetically) different communities are. The observed patterns can then be interpreted in terms of environmental gradients, geographical distributions, etc.

Note that the combination of the components $\sum_{ij} x_i z_j \sigma_{ij}$, $\sum_{ij} x_i x_j \sigma_{ij}$ and $\sum_{ij} z_i z_j \sigma_{ij}$ into a similarity index does not necessarily lead to p.s.d. matrices. For example, Ricotta and Szeidl (2009) defined the dissimilarity among a collection of communities as $\hat{\beta} = \hat{\gamma}/\hat{\alpha}$. When applied to a pair of communities with their respective vectors of species' proportions **p** and **q**, then

$$\hat{\gamma} = 1/\left[1 - Q\left(\frac{\mathbf{p} + \mathbf{q}}{2}\right)\right] \qquad \text{eqn 10}$$

$$\hat{\alpha} = 1/\left[1 - \frac{1}{2}Q(\mathbf{p}) - \frac{1}{2}Q(\mathbf{q})\right] \qquad \text{eqn 11}$$

If $\mathbf{\Delta} = (\delta_{ij})$ is squared Euclidean, the coefficient $\hat{\gamma}/\hat{\alpha}$ is not bounded between 0 and 1 but between 1 and 2. This is because the objective of Ricotta and Szeidl (2009) was to obtain an effective number of communities: if community A is identical to community B, we actually have only one community, such that $\hat{\gamma}/\hat{\alpha} = 1$. On the other hand, if both communities are completely distinct $\hat{\gamma}/\hat{\alpha} = 2$. Therefore, a simple solution to obtain a dissimilarity coefficient bounded between 0 and 1, within the Ricotta and Szeidl framework, is to define $D_\beta = \hat{\gamma}/\hat{\alpha} - 1$, which can be written as:

$$D_\beta = \frac{\frac{1}{2}\sum_{ij} p_i q_j \delta_{ij} - \frac{1}{4}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{4}\sum_{ij} q_i q_j \delta_{ij}}{1 - \frac{1}{2}\sum_{ij} p_i q_j \delta_{ij} - \frac{1}{4}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{4}\sum_{ij} q_i q_j \delta_{ij}} \qquad \text{eqn 12}$$

Because D_β is bounded between 0 and 1, an associated similarity coefficient can be defined as $S_\beta = 1 - D_\beta$. Using interspecies similarities instead of dissimilarities, the expression of S_β simplifies to:

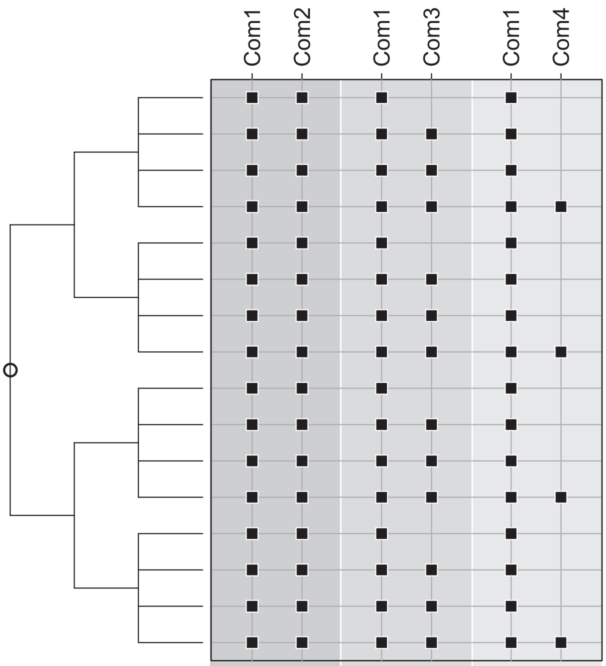
$$S_\beta = \frac{4\sum_{ij} p_i q_j \sigma_{ij}}{2\sum_{ij} p_i q_j \sigma_{ij} + \sum_{ij} p_i p_j \sigma_{ij} + \sum_{ij} q_i q_j \sigma_{ij}} \qquad \text{eqn 13}$$

where $\sigma_{ij} = 1 - \delta_{ij}$ for all *i*, *j* are pairwise (functional or phylogenetic) similarities among species. Formula S_β thus combines $\sum_{ij} p_i q_j \sigma_{ij}$, $\sum_{ij} p_i p_j \sigma_{ij}$ and $\sum_{ij} q_i q_j \sigma_{ij}$ into an index of similarity bounded between 0 and 1. However, this index does not lead to intercommunity similarity matrices that are p.s.d. (a counter-example is given in the demonstration of the use of the R scripts in Appendix S3). Here, note that, while the similarity counterpart of the index D_β, $S_\beta = 1 - D_\beta$ is generally not p.s.d., nonetheless we have $S_\beta = \theta_i/(\theta_i - 1 + 1/S_i)$, with $\theta_1 = 8$ and $S_1 = S_{Sokal\text{-}Sneath}$, $\theta_2 = 4$ and $S_2 = S_{Jaccard}$, $\theta_3 = 2$ and $S_3 = S_{Sørensen}$. Note also that S_β is equivalent to the phylo-regional-overlap index of Chiu, Jost and Chao (2014) applied to two communities only and extended to any type of (taxonomic, phylogenetic or functional) similarities among species (section 1.6 in Appendix S1). Preliminary analysis suggests that the behaviour of S_β is similar to $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}, although it tends to provide higher similarity values (as illustrated in the examples for the use of the R scripts in Appendix S3). We have thus not included S_β in our case studies.

CASE STUDIES

We first compared indices $S_Q = 1 - D_Q$, $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai} with COMDIST and the associated similarity index, 1-COMDIST, on a small theoretical data set as described in Fig. 1. After having illustrated the strong difference between COMDIST and the behaviour of the other indices, we then concentrated on the latter ones. Note that as S_Q and COMDIST depend on species' proportions, vectors x and z in the equations of $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai} were expressed as proportions in all our case studies.

To compare indices S_Q, $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}, we considered the data set analysed in Ivol *et al.* (1997) and Pavoine and Dolédec (2005) where a total of 40 macroinvertebrate species (here Coleoptera and Trichoptera) were sampled in 38 stations distributed in the Loire River (France) from the spring to 200 km upstream of the mouth. Stations have been sampled in July 1989 and 1991, and in March and May 1993, in rubble riffle habitats with a hand-net for about 10 min per station. Individuals were identified at the species level and counted. The objective here was not to re-analyse an old data set but rather to show where the indices of similarity proposed in Table 2



Dissimilarity Index			
COMDIST	0·729	0·729	0·729
Similarity Indices			
1-COMDIST	0·271	0·271	0·271
$S_{Sokal\text{-}Sneath}$	1	0·951	0·684
$S_{Jaccard}$	1	0·975	0·813
$S_{Sørensen}$	1	0·987	0·897
S_{Ochiai}	1	0·987	0·901
S_Q	1	0·997	0·969

Fig. 1. Behavior of COMDIST for a small data set composed of four communities (Com1–Com4). Top left: theoretical phylogenetic tree with equal branch lengths and species as tips. The height of the tree (sum of branch lengths on the smallest path between tips and root) was considered to be unity. An open circle indicates the root node of the phylogeny. Top right: compositions of the four communities. Close squares represent species presences. Bottom: Index values of COMDIST and six similarity measures among communities (all measures are calculated with species proportions equal to $1/N_i$, where N_i is the number of species in the ith community). As COMDIST is bounded between 0 and 1 (because interspecific dissimilarities among species, themselves varied between 0 and 1), we also included 1-COMDIST among the similarity measures.

behave similarly and where they do not. We performed two distinct analyses.

In the first analysis, the index $S_Q = 1 - D_Q$ was compared to $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai} using the real data set. First, similarities among stations were evaluated by considering only the relative number of individuals from each species collected in each station. Then, similarities among species were considered using taxonomy and feeding habits. The taxonomic tree was considered with unit branch length and the root placed at the class level (Insecta) assuming that species of the order Coleoptera have zero taxonomic similarity with Trichoptera species. The index used to calculate the taxonomic similarities among species was related to that used to calculate taxonomic similarities among stations. For example, for calculating the index $S_{Sokal\text{-}Sneath}$, we used the following index of interspecific similarity: for any two species i and j, $\sigma_{ij} = a/(a + 2b + 2c)$ where a = sum of branch lengths from the nearest common ancestor of the two species i and j to the root of the tree, b = sum of branch lengths from species i to this nearest common ancestor and c = sum of branch lengths from species j to this nearest common ancestor. Using the same notation, the indices of interspecific similarity $a/(a + b + c)$, $2a/(2a + b + c)$ and $a/\sqrt{(a+b)(a+c)}$ were used for calculating $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}, respectively. In general, we suggest the use of consistent indices for measuring the similarity among species and among communities since this is allowed by our methodology (Appendix S2). The indices $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai} were then compared with S_Q. For comparing S_Q with, say, $S_{Sokal\text{-}Sneath}$, we calculated S_Q using the same measure of interspecies similarity used for calculating $S_{Sokal\text{-}Sneath}$. The same procedure was used for all pairwise comparisons between S_Q and one of the newly proposed measures.

Regarding feeding habits, the affinity of each species to each feeding category (engulfers, shredders, scrapers, deposit-feeders, active filter-feeders, passive filter-feeders and piercers) was quantified using a fuzzy coding approach (Chevenet, Dolédec & Chessel 1994). The species affinity for each feeding category was estimated by expert opinion on an ordinal scale ranging from 0 (no affinity) to 3 (high affinity; Ivol *et al.* 1997). The similarity between two species was then calculated using Table 2, second column, by replacing the vectors of species' proportions in each community with vectors showing the species relative affinities for each feeding category. For example, the index $S_{Sokal\text{-}Sneath}$ was calculated using the following index of interspecific similarity: for any two species i and j,

$$\sigma_{ij} = \sum\nolimits_k a_{ik}a_{jk} \Big/ \left(2\sum\nolimits_k a_{ik}^2 + 2\sum\nolimits_k a_{jk}^2 - 3\sum\nolimits_k a_{ik}a_{jk}\right) \qquad \text{eqn 14}$$

where a_{ik} and a_{jk} are the relative affinities of species i and j to the kth feeding category. Using the same notation, the indices of interspecies similarity $\sigma_{ij} = \sum_k a_{ik}a_{jk}/(\sum_k a_{ik}^2 + \sum_k a_{jk}^2 - \sum_k a_{ik}a_{jk})$, $\sigma_{ij} = 2\sum_k a_{ik}a_{jk}/(\sum_k a_{ik}^2 + \sum_k a_{jk}^2)$, and $\sigma_{ij} = \sum_k a_{ik}a_{jk}/\sqrt{\sum_k a_{ik}^2 \sum_k a_{jk}^2}$ were used for calculating $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}, respectively. These indices were then compared with S_Q. For the calculation of S_Q, we used the same measure of interspecies similarity used for calculating the corresponding similarity measures $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}.

In the second analysis, the behaviour of $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai} was analysed in more details using the theoretical data in Fig. 2. We also calculated four different versions of S_Q, each with a different measure of interspecies similarity (for details see Table 3).

We first used the same taxonomy as in the real data set. Next, we distorted it by attributing different branch lengths to the taxonomic levels. The theoretical communities associated with the taxonomy in Fig. 2 included only the presence/absence of species. Two of them contained only Coleoptera (communities 1 and 2), while the other two communities contained Trichoptera only (communities 3 and 4). Each community contained a species per family and, when possible (i.e. when more than one species was represented per family), different species were attributed to different communities. Taxonomic similarities among species and among communities were calculated with the same procedure as for the real data set. Only communities 3 and 4 have some species in common. We thus expected their taxonomic similarity to be the highest. Because communities 1 and 2 contain Coleoptera only and communities 3 and 4 Trichoptera only, we expected the similarity of community 1 (or 2) with community 3 (or 4) to be the lowest. The data set was designed so that the similarities between communities with Coleoptera only and communities with Trichoptera only (i.e. communities 1 × 3, 1 × 4, 2 × 3, and 2 × 4) were all equal.

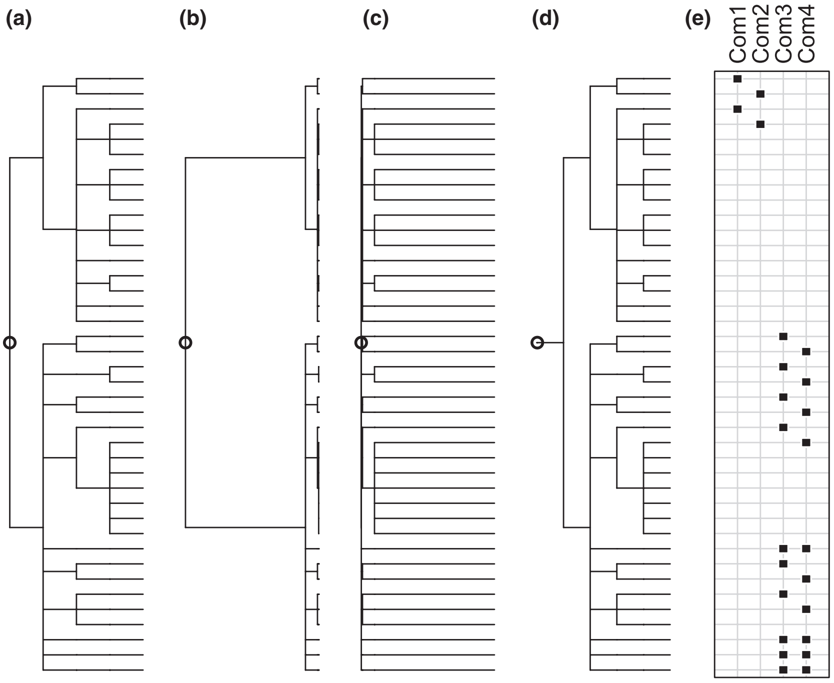


Fig. 2. Theoretical data set. (a) The taxonomy of the real data set with equal branch lengths. The first split in the taxonomy is at the order-level (top: Coleoptera, bottom: Trichoptera). Subsequent splits represent families, genera and species (tips). (b–d) The taxonomy was then deformed by adjusting the branch lengths so that the similarities among species are increased (b) and decreased (c). In (d) equal branch lengths are considered, together with an additional taxonomic level (*e.g.* phylum = Arthropoda) common to all species. This added taxonomic level increases the similarities among all species. Open circles indicate the root node of the taxonomies. The taxonomic height of all trees (sum of branch lengths on the shortest path between tips and root) was considered equal to unity. These taxonomies were associated with four theoretical communities defined in (e). Close squares indicate species presences within each community.

Results

Using COMDIST, the same value of dissimilarity was found between communities 1 and 2, between communities 1 and 3 and between communities 1 and 4 in Fig. 1. In contrast, the indices $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$, S_{Ochiai} and S_Q correctly identify that communities 1 and 2 are identical and that community 1 shows decreasing similarity with communities 2, 3 and 4 in that order (Fig. 1).

The real data set showed discrepancies between S_Q and the other indices when species were considered to be completely distinct from each other (i.e. $\sigma_{ij} = 0$ for all $i \neq j$; Fig. 3a). These differences decreased when taxonomic and functional similarities among species were added (Fig. 3b,c). Taken together, despite some fundamental differences between S_Q and the new indices, like the shape of the relationships and the spread of points in Fig. 3, in general, S_Q had high Spearman correlation with the other indices. S_Q and the new indices would thus tend to rank, at least with this data set, the similarities among communities in consistent ways. Situations where S_Q was positive whereas the other indices equal zero were observed only between a few sites when taxonomic similarities among species were used (Fig. 3b).

As expected, with the theoretical data set in Fig. 2, communities 3 and 4 had the highest taxonomic similarity (Table 3). Also, for all scenarios of taxonomic branch lengths, all indices $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}, attributed the lowest values of taxonomic similarity between communities with Coleoptera only and communities with Trichoptera only (named C × T in Table 3). However, with the index S_Q, we obtained higher similarity values between two communities composed of species from different orders than between two communities composed of Coleoptera only. This happened when S_Q was calculated using the index of interspecies similarity associated with $S_{Sokal\text{-}Sneath}$. It also happened, whatever the index of interspecies similarity, when the similarities among species were low. Overall, the analysis revealed that the impact of the index chosen for summarizing pairwise community similarity can be drastic. For example, using the phylogeny with equal branch lengths (Fig. 2a), the similarity between communities 1 and 2 is equal to 0·080 for the index $S_{Sokal\text{-}Sneath}$ and 0·600 for S_{Ochiai}.

Discussion

DIFFERENCES BETWEEN 1-COMDIST, S_Q, AND THE NEW INDICES

Our results first highlighted a difference in behaviour between 1-COMDIST and the other indices. A criticism that can be raised towards COMDIST (and thus 1-COMDIST, Webb, Ackerly & Kembel 2008) is that it would provide equal levels of dissimilarity between two identical communities as between two communities with distinct species. This unexpected behav-

Table 3. Taxonomic similarities among the theoretical communities in Fig. 2

	Similarity indices among communities (S) and among species (σ)						
	$S_{Sokal\text{-}Sneath}$	S_Q calculated with $\sigma_{Sokal\text{-}Sneath}$	S_{Jaccard}	S_Q calculated with $\sigma_{Jaccard}$	$S_{Sørensen}$	S_{Ochiai}	S_Q calculated with $\sigma_{Sørensen\,(=\sigma_{Ochiai})}$
Uniform model							
Com 1 × 2	0·080	**0·600**	0·263	0·667	0·600	0·600	0·750
Com 3 × 4	0·403	0·954	0·719	0·963	0·915	0·915	0·973
Com C × T	0	0·646	0	0·600	0	0	0·525
High interspecific similarity model							
Com 1 × 2	0·914	0·981	0·978	0·990	0·995	0·995	0·995
Com 3 × 4	0·989	0·998	0·998	0·999	0·999	0·999	0·999
Com C × T	0	0·215	0	0·127	0	0	0·070
Low interspecific similarity model							
Com 1 × 2	0·001	**0·501**	0·003	**0·503**	0·011	0·011	**0·505**
Com 3 × 4	0·146	0·940	0·258	0·941	0·420	0·420	0·942
Com C × T	0	0·700	0	0·700	0	0	0·700
Uniform model and additional taxonomic level							
Com 1 × 2	0·125	**0·636**	0·373	0·714	0·714	0·714	0·800
Com 3 × 4	0·531	0·959	0·821	0·968	0·952	0·952	0·978
Com C × T	0·041	0·659	0·132	0·636	0·345	0·352	0·620

Interspecific similarities were defined as, $\sigma_{Sokal\text{-}Sneath} = a/(a + 2b + 2c)$, $\sigma_{Jaccard} = a/(a + b + c)$, $\sigma_{Sørensen} = 2a/(2a + b + c)$, $\sigma_{Ochiai} = a/\sqrt{(a+b)(a+c)}$, with a = sum of branch lengths from the nearest common ancestor of two species to the root of the tree, b = sum of branch lengths from the first species to this nearest common ancestor and c = sum of branch lengths from the second species to this nearest common ancestor. Given the ultrametric tree in this particular example, $\sigma_{Sørensen} = \sigma_{Ochiai}$. Also, wherever the average similarities among species within compared communities are equal, $S_{Sørensen} = S_{Ochiai}$. Com 1 × 2 is the similarity among the Coleoptera communities (Com1 and Com 2) and Com 3 × 4 is the similarity among the Trichoptera communities (Com3 and Com4). Com C × T is the similarity between a community composed of Coleoptera only (either Com1 or Com2) and a community composed of Trichoptera only (either Com3 or Com4). Bold values indicate situations where Com 1 × 2 or Com 3 × 4 < Com C × T. Note that the data set in Fig. 2 was designed so that the similarities between communities with Coleoptera only and communities with Trichoptera only (i.e. communities 1 × 3, 1 × 4, 2 × 3, and 2 × 4) were all equal.

iour for an index of dissimilarity among communities is due to the fact that COMDIST is an absolute index. Indeed it calculates how different species from two distinct communities are without considering how different species from the same community are. When measuring (dis)similarities among communities, it is thus important to compare how (dis)similar species from different communities are with the level of (dis)similarity among species from the same community.

In addition, the real data set confirmed that S_Q behaves differently from the other indices when species are treated as maximally different (*i.e.* zero similarity among species). We also found very few maximally dissimilar stations (absence of similarities between species from distinct stations). Such scenarios of maximally dissimilar communities are likely to be infrequent in ecological studies that incorporate similarities among species, at least at local scales.

However, our simulations showed that the existence of maximally dissimilar species (and thus of maximally dissimilar sites) did not increase the differences between S_Q and the other indices. For instance, all indices tended to have close behaviour when the similarities among species were artificially and drastically increased. In contrast, S_Q showed distinct values when the interspecific similarities were decreased. By adding a taxonomic level, we increased similarities among species and eliminated the existence of maximally dissimilar species, but in spite of that, S_Q still provided high taxonomic similarity between stations with only Coleoptera and stations with only Trichoptera. In contrast, the new indices acknowledged low similarities between these stations. The values of S_Q also depended to some extent on the coefficients used to calculate the taxonomic and functional similarities among species. This does not mean that S_Q is meaningless. As highlighted by Pavoine, Dufour and Chessel (2004), D_Q (= 1 − S_Q) can be viewed as the distance between the centroids of two communities in a multidimensional space where species are positioned according to their functional or phylogenetic distances. It is now well-established that a single index cannot summarize all aspects of biodiversity. The same conclusion holds for (dis)similarity indices.

Comparing the new indices $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$ and S_{Ochiai}, we showed that all indices tend to rank communities similarly. However, the index values can be very different. This might be annoying if one interprets the index values in an intuitive way, from 0 meaning no similarity to 1 meaning complete similarity. Two data sets can thus be compared only if the same index is used. On the other hand, as the different indices have slightly different properties, they allow calculating community similarity from different viewpoints and perspectives. The differences among the indices only depend on how the three components $\sum_{ij} x_i z_j \sigma_{ij}$ (similarity among the species in different communities), $\sum_{ij} x_i x_j \sigma_{ij}$ (similarity among the species in the first community) and $\sum_{ij} z_i z_j \sigma_{ij}$ (similarity among the species in the second community) are combined into an index of similarity. For example, both indices S_{Ochiai} and

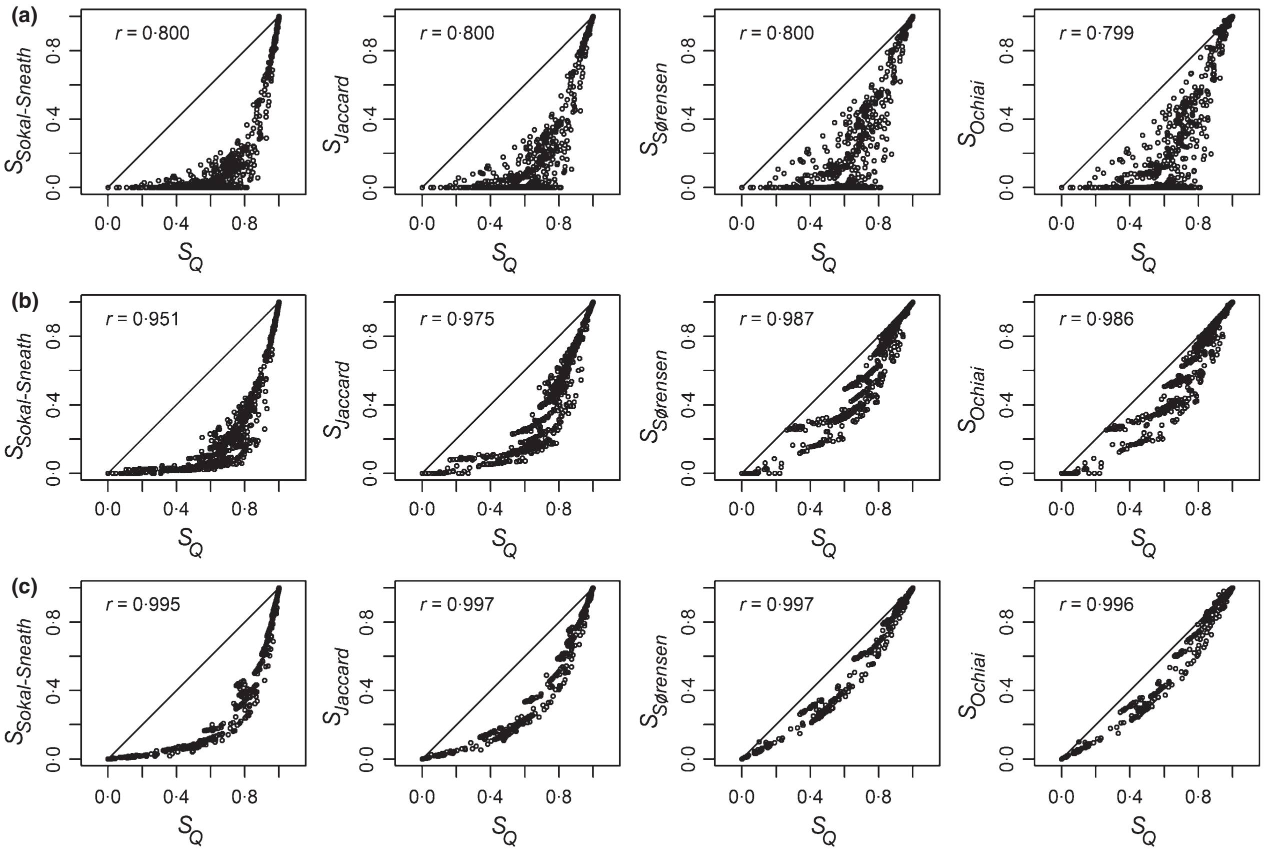


Fig. 3. Scatterplots between the new indices and the index S_Q applied to the real data set considering (a) minimum (zero) similarity among species; (b) taxonomic similarity; and (c) similarities in feeding habits. Spearman correlations between the new indices and S_Q are indicated on each panel.

$S_{Sørensen}$ compare the similarity among the species in different communities (numerator) with the average similarity among the species in the same community (denominator). However, by substituting the geometric mean for the arithmetic mean of $\sum_{ij} x_i x_j \sigma_{ij}$ and $\sum_{ij} z_i z_j \sigma_{ij}$ in $S_{Sørensen}$ compared with S_{Ochiai}, the contribution of the species similarity within two communities to the value of the index is decreased just because the geometric mean leads to lower values than the arithmetic mean. From this point of view, the denominator of $S_{Sokal\text{-}Sneath}$ and $S_{Jaccard}$ does not contain solely the average similarities among species within communities but rather the difference between these similarities and the similarity among the species in different communities. Accordingly, in $S_{Sokal\text{-}Sneath}$ and $S_{Jaccard}$, the relevance of the similarities among the species in different communities is decreased compared to the similarities within communities.

Altogether, the interests of the new family of indices are thus (i) to extend traditional similarity measures to taxonomic, phylogenetic or functional similarities among species and communities; (ii) to be flexible in the choice of the species' weights (presence/absence, individual counts/biomass, relative abundance, etc.) and in the definition of similarities among species that can be computed in many different ways from taxonomy, phylogeny, functional dendrograms and functional data sets that can contain nominal, quantitative, binary, proportional and fuzzy variables (Appendix S2); and (iii) to provide a particular treatment of maximally dissimilar communities.

A last remark can be made on the development of this family of indices. Indices in columns 4 of Table 2 can be applied to vectors of species presences/absences within communities but also to any set of elements including evolutionary units (which would lead to the indices of Lozupone and Knight 2005 and Ferrier *et al.* 2007) for measuring the phylogenetic similarity between communities, and volumes in functional spaces (which would embed the index of Villéger, Novack-Gottshall & Mouillot 2011) for measuring the functional similarity between communities.

THE NEW FAMILY AS A UNIFIED FRAMEWORK FOR FUNCTIONAL SIMILARITY AND PHYLOGENETIC SIMILARITY INDICES

A previous paper showed that, when comparing functional diversity with phylogenetic diversity, the same mathematical indices should be used to avoid the risk of misinterpreting differences in functional and phylogenetic diversity by biological processes when the differences are just mathematical artefacts (Pavoine *et al.* 2013). This remark is also true for functional and phylogenetic similarity indices. This is why we developed here a methodological framework that can apply to functional similarities or to (taxonomic) phylogenetic similarities among species and communities.

Among the indices of intercommunity similarity developed in the literature, some have been designed for functional traits (Villéger, Novack-Gottshall & Mouillot 2011), and others for phylogenies (Lozupone & Knight 2005; Ferrier *et al.* 2007; Pavoine, Love & Bonsall 2009; Ives & Helmus 2010; Nipperess, Faith & Barton 2010; Chiu, Jost & Chao 2014). On the contrary, Rao's D_Q has been suggested to measure any type of dissimilarity including taxonomic, genetic, phylogenetic and functional similarity (Nei & Li 1979; Rao 1982; Izsák & Papp 1995; Pavoine & Dolédec 2005; Ricotta 2005).

Many indices developed within the functional or phylogenetic context can be easily transposed to the other type of data (Pavoine & Bonsall 2011). While the development of traditional diversity indices was mainly interdisciplinary, the addition of functional vs. phylogenetic (dis)similarities among species has split research on diversity and (dis)similarity measures. The main difficulty when comparing functional and phylogenetic data is that phylogenetic data intrinsically imply a tree-shaped structure among species. For example, the indices developed by Lozupone and Knight (2005), Ferrier *et al.* (2007), Pavoine, Love and Bonsall (2009), Nipperess, Faith and Barton (2010), and Chiu, Jost and Chao (2014) depend on tree-shaped structures among species (phylogenies). In general, functional data might thus be used with these indices only if they are artificially transformed into functional dendrograms using clustering approaches as suggested by Petchey and Gaston (2002). Such approaches add methodological choices and the distortion of the data might be high when one or a few functional traits only are considered. This is because a tree is a multidimensional object (e.g. Nabben & Varga 1994), whereas a quantitative trait can be displayed in one only dimension. In contrast, our family of similarity indices can be used with many different data types provided similarity among species is bounded between 0 and 1.

Some of the solutions proposed to develop functional indices implied to transform functional data into the form of data traditionally used to measure compositional similarity among communities. For example, Robertson, McAlpine and Maron (2013) used a *species* × *trait* matrix to define functional groups. Then, they applied the Bray–Curtis index (Bray & Curtis 1957) on log-transformed summed densities of all members of functional groups. In a phylogenetic context, this solution could be adapted by measuring the Bray–Curtis index on log-transformed summed densities/abundances/biomasses of all members of clades. However, in comparison with our indices, this solution considers all functional groups (or clades) as maximally dissimilar, which is not always the case.

In conclusion, we have introduced a new family of similarity indices that is very flexible in the type of data used. By designing this family, we advised, wherever possible, for the use of coherent indices for measuring similarities among species and similarities among communities; for the use of relative similarity indices that integrate the diversity of the community and that are bounded between 0 and 1; and for the use of p.s.d. indices. This family embeds a large variety of similarity indices developed so far for measuring species, functional or phylogenetic diversity and (dis)similarity.

Acknowledgements

We thank János Podani and an anonymous reviewer for their comments. They both contributed to improve our paper.

Data accessibility

Data are available in the R package ade4 (Chessel, Dufour & Thioulouse 2004; R Development Core Team 2013). An R script can be uploaded as online supporting information (Appendix S4). The R script for the index COMDIST is available in the R package picante (Kembel *et al.* 2010).

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Received 27 November 2013; accepted 1 April 2014
Handling Editor: David Orme

Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Proofs.

Appendix S2. How to calculate similarities among species.

Appendix S3. Manual for R functions and examples of their use.

Appendix S4. R scripts for functions.

Appendix S5. R scripts for examples.

Supporting Information

1 Appendix S1. Proofs

1.1 Formula for index S_{st}

$$D_{st} = \frac{\sum_{ij} p_i q_j \delta_{ij} - \frac{1}{2}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{2}\sum_{ij} q_i q_j \delta_{ij}}{1 - \frac{1}{2}\sum_{ij} p_i p_j \delta_{ij} - \frac{1}{2}\sum_{ij} q_i q_j \delta_{ij}}$$

Replacing δ_{ij} with $1 - \sigma_{ij}$ leads to

$$D_{st} = \frac{\frac{1}{2}\sum_{ij} p_i p_j \sigma_{ij} + \frac{1}{2}\sum_{ij} q_i q_j \sigma_{ij} - \sum_{ij} p_i q_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} p_i p_j \sigma_{ij} + \frac{1}{2}\sum_{ij} q_i q_j \sigma_{ij}}$$

Finally, considering $S_{st} = 1 - D_{st}$ leads to

$$S_{st} = 1 - \frac{\frac{1}{2}\sum_{ij} p_i p_j \sigma_{ij} + \frac{1}{2}\sum_{ij} q_i q_j \sigma_{ij} - \sum_{ij} p_i q_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} p_i p_j \sigma_{ij} + \frac{1}{2}\sum_{ij} q_i q_j \sigma_{ij}}$$

$$S_{st} = \frac{\sum_{ij} p_i q_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} p_i p_j \sigma_{ij} + \frac{1}{2}\sum_{ij} q_i q_j \sigma_{ij}}$$

1.2 Index $S_{Sørensen}$ is related to Chiu, Jost & Chao (2013) phylo-Morisita-Horn index

Consider a set of n species and their ultrametric phylogenetic tree. Let $\mathbf{\Delta}$ be the matrix of phylogenetic distances among species (sum of branch lengths between two species and their nearest common ancestor). Let T be the height of the phylogenetic tree studied (not necessarily defined at the nearest common ancestor of all species included in the phylogeny). Let $\mathbf{p}$ and $\mathbf{q}$ be species' proportions within two communities. When applied to the comparison of 2 balanced communities only (with equal weights), and to an ultrametric tree, Chiu, Jost & Chao (2013) phylo-Morisita-Horn index is equal to

$$1 - 2\frac{Q_\gamma - Q_\alpha}{(T - Q_\alpha)}$$

which can also be written as

$$1 - 2\frac{Q_\gamma/T - Q_\alpha/T}{(1 - Q_\alpha/T)}$$

where

$$Q_\alpha = \frac{1}{2}\mathbf{p}^t\mathbf{\Delta}\mathbf{p} + \frac{1}{2}\mathbf{q}^t\mathbf{\Delta}\mathbf{q}$$

and

$$Q_\gamma = \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)^t \mathbf{\Delta} \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)$$

In this equation,

$$Q_\gamma - Q_\alpha = \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)^t \mathbf{\Delta} \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right) - \frac{1}{2}\mathbf{p}^t\mathbf{\Delta}\mathbf{p} - \frac{1}{2}\mathbf{q}^t\mathbf{\Delta}\mathbf{q}$$

which simplifies to

$$Q_\gamma - Q_\alpha = \frac{1}{2}\mathbf{p}^t\mathbf{\Delta}\mathbf{q} - \frac{1}{4}\mathbf{p}^t\mathbf{\Delta}\mathbf{p} - \frac{1}{4}\mathbf{q}^t\mathbf{\Delta}\mathbf{q}$$

Consider $\mathbf{\Sigma} = \mathbf{1}\mathbf{1}^t - \mathbf{\Delta}/T$, where $\mathbf{1}$ is a unit vector.

$$Q_\gamma/T - Q_\alpha/T = \frac{1}{2}\mathbf{p}^t\left(\mathbf{1}\mathbf{1}^t - \mathbf{\Sigma}\right)\mathbf{q} - \frac{1}{4}\mathbf{p}^t\left(\mathbf{1}\mathbf{1}^t - \mathbf{\Sigma}\right)\mathbf{p} - \frac{1}{4}\mathbf{q}^t\left(\mathbf{1}\mathbf{1}^t - \mathbf{\Sigma}\right)\mathbf{q}$$

$$Q_\gamma/T - Q_\alpha/T = \frac{1}{4}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{4}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q} - \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}$$

In addition,

$$1 - Q_\alpha/T = 1 - \frac{1}{2}\mathbf{p}^t\left(\mathbf{1}\mathbf{1}^t - \mathbf{\Sigma}\right)\mathbf{p} - \frac{1}{2}\mathbf{q}^t\left(\mathbf{1}\mathbf{1}^t - \mathbf{\Sigma}\right)\mathbf{q}$$

which simplifies to

$$1 - Q_\alpha/T = \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{2}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q}$$

It follows that

$$\frac{(Q_\gamma/T - Q_\alpha/T)}{1 - Q_\alpha/T} = \frac{1}{2} - \frac{\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}}{\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \mathbf{q}^t\mathbf{\Sigma}\mathbf{q}}$$

and

$$1 - 2\frac{Q_\gamma - Q_\alpha}{(T - Q_\alpha)} = \frac{2\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}}{\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \mathbf{q}^t\mathbf{\Sigma}\mathbf{q}} = S_{Sørensen}$$

1.3 The similarity indices vary between 0 and 1

We consider positive semi-definite (p.s.d) matrices $\mathbf{\Sigma}$. With this property, there exists a matrix $\mathbf{R}$ so that $\mathbf{\Sigma} = \mathbf{R}\mathbf{R}^t$ (Seber, 2008, p. 221). Considering $\mathbf{u} = \mathbf{R}^t\mathbf{x}$ and $\mathbf{v} = \mathbf{R}^t\mathbf{z}$, index $S_{Sørensen}$ can be rewritten as

$$\frac{\mathbf{u}^t\mathbf{v}}{\frac{1}{2}\left(\mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v}\right)}$$

The parallelogram law states that $||\mathbf{u}+\mathbf{v}||^2 = 2||\mathbf{u}||^2 + 2||\mathbf{v}||^2 - ||\mathbf{u}-\mathbf{v}||^2$, with $||.||$ the L2-norm. This implies that

$$(\mathbf{u}+\mathbf{v})^t(\mathbf{u}+\mathbf{v}) \leq 2\mathbf{u}^t\mathbf{u} + 2\mathbf{v}^t\mathbf{v}$$
$$2\mathbf{u}^t\mathbf{v} + \mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v} \leq 2\mathbf{u}^t\mathbf{u} + 2\mathbf{v}^t\mathbf{v}$$
$$\mathbf{u}^t\mathbf{v} \leq \frac{1}{2}\left(\mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v}\right)$$

$S_{Sørensen}$ thus varies between 0 and 1.

Given that

$$\mathbf{u}^t\mathbf{v} \leq \frac{1}{2}\left(\mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v}\right)$$

then

$$2\mathbf{u}^t\mathbf{v} \leq \mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v}$$

and

$$\mathbf{u}^t\mathbf{v} \leq \mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v} - \mathbf{u}^t\mathbf{v}$$

so that $S_{Jaccard}$ varies between 0 and 1.

Similarly,

$$4\mathbf{u}^t\mathbf{v} \leq 2\mathbf{u}^t\mathbf{u} + 2\mathbf{v}^t\mathbf{v}$$

so that

$$\mathbf{u}^t\mathbf{v} \leq 2\mathbf{u}^t\mathbf{u} + 2\mathbf{v}^t\mathbf{v} - 3\mathbf{u}^t\mathbf{v}$$

and $S_{Sokal-Sneath}$ varies between 0 and 1.

The Cauchy-Schwarz inequality proves that S_{Ochiai} varies between 0 and 1 (Seber, 2008, p. 258).

1.4 The similarity matrices are p.s.d.

The proofs for $S_{Sørensen}$ and S_{Ochiai} are given by Zegers & ten Berge (1985) considering the vectors $\mathbf{u}$ and $\mathbf{v}$ defined in section 1.3.

The proofs for $S_{Sokal-Sneath}$ and $S_{Jaccard}$ derive from $S_{Sørensen}$ being p.s.d and from Gower & Legendre (1986) demonstration in the particular case where only presences/absences are concerned. The demonstration below follows Gower & Legendre (1986): Indeed let $x = \mathbf{u}^t\mathbf{v}$, and $y = \mathbf{u}^t\mathbf{u} + \mathbf{v}^t\mathbf{v} - 2\mathbf{u}^t\mathbf{v}$. Consider

$$R_\phi = \frac{x}{x + \phi y}$$

$S_{Sørensen}$ is equal to $R_{\frac{1}{2}}$, $S_{Jaccard}$ to R_1, and $S_{Sokal-Sneath}$ to R_2.

Let $\theta \leq \phi$; R_ϕ may be manipulated into

$$R_\phi = \frac{x\theta/\phi}{x + \theta y}\left[1 - \left(1 - \frac{\theta}{\phi}\right)\frac{x}{x + \theta y}\right]^{-1}$$

Expanding shows that the similarity matrices $\mathbf{R}_\phi$ and $\mathbf{R}_\theta$ (with pairwise applications of R_ϕ and R_θ for any x and y) are related by:

$$\mathbf{R}_\phi = \frac{\theta}{\phi}\mathbf{R}_\theta{}^\circ\left[\mathbf{1}\mathbf{1}^t + \psi\mathbf{R}_\theta + \psi^2\mathbf{R}_\theta^{(2)} + \psi^3\mathbf{R}^{(3)} + ...\right]$$

where $\psi = 1 - \theta/\phi$, $\mathbf{1}$ is a unit vector, $^\circ$ is the Hadamard product, and $\mathbf{R}^{(2)} = \mathbf{R}^\circ\mathbf{R}$, etc. If two matrices are p.s.d. then so is their Hadamard product (Schur's theorem). The sum of two symmetric p.s.d matrices is p.s.d. It follows that $\mathbf{R}_\phi$ is p.s.d. wherever $\mathbf{R}_\theta$ (where $\theta \leq \phi$, *i.e.* $\psi \geq 0$) is p.s.d.

1.5 $S_{Sokal-Sneath} \leq S_{Jaccard} \leq S_{\boldsymbol{Sørensen}} \leq S_{Ochiai}$

$S_{Sørensen} \leq S_{Ochiai}$ follows directly from the fact that the arithmetic mean provides higher values than the geometric mean. Hereafter, we consider that the numerator of $S_{Sokal-Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$, and S_{Ochiai} is $\mathbf{x\Sigma z}$.

Let $B_{Sokal-Sneath}$ be the denominator of $S_{Sokal-Sneath}$:

$$B_{Sokal-Sneath} = 2\mathbf{x}^t\mathbf{\Sigma x} + 2\mathbf{z}^t\mathbf{\Sigma z} - 3\mathbf{x}^t\mathbf{\Sigma z}$$

Let $B_{Jaccard}$ be the denominator of $S_{Jaccard}$:

$$B_{Jaccard} = \mathbf{x}^t\mathbf{\Sigma x} + \mathbf{z}^t\mathbf{\Sigma z} - \mathbf{x}^t\mathbf{\Sigma z}$$

Let $B_{Sørensen}$ be the denominator of $S_{Sørensen}$:

$$B_{Sørensen} = \frac{1}{2}\mathbf{x}^t\mathbf{\Sigma x} + \frac{1}{2}\mathbf{z}^t\mathbf{\Sigma z}$$

Given that $\mathbf{\Sigma}$ is p.s.d., $\frac{1}{2}\mathbf{x}^t\mathbf{\Sigma x} + \frac{1}{2}\mathbf{z}^t\mathbf{\Sigma z} - \mathbf{z}^t\mathbf{\Sigma z} \geq 0$(see above).

$$B_{Sokal-Sneath} \geq B_{Jaccard} \Leftrightarrow 2\mathbf{x}^t\mathbf{\Sigma x} + 2\mathbf{z}^t\mathbf{\Sigma z} - 3\mathbf{x}^t\mathbf{\Sigma z} \geq \mathbf{x}^t\mathbf{\Sigma x} + \mathbf{z}^t\mathbf{\Sigma z} - \mathbf{x}^t\mathbf{\Sigma z}$$

$$\Leftrightarrow \mathbf{x}^t\mathbf{\Sigma x} + \mathbf{z}^t\mathbf{\Sigma z} - 2\mathbf{z}^t\mathbf{\Sigma x} \geq 0$$

$$B_{Jaccard} \geq B_{Sørensen} \Leftrightarrow \mathbf{x}^t\mathbf{\Sigma x} + \mathbf{z}^t\mathbf{\Sigma z} - \mathbf{x}^t\mathbf{\Sigma z} \geq \frac{1}{2}\mathbf{x}^t\mathbf{\Sigma x} + \frac{1}{2}\mathbf{z}^t\mathbf{\Sigma z}$$

$$\Leftrightarrow \frac{1}{2}\mathbf{x}^t\mathbf{\Sigma x} + \frac{1}{2}\mathbf{z}^t\mathbf{\Sigma z} - \mathbf{z}^t\mathbf{\Sigma x} \geq 0$$

1.6 S_β is related to Chiu et al. (2013) phylo-regional-overlap index

Considering the same notations as in the section 1.2, two balanced communities only (with equal weights), and an ultrametric tree, Chiu, Jost & Chao (2013) phylo-regional-overlap index is equal to

$$1 - \frac{Q_\gamma - Q_\alpha}{(T - Q_\gamma)}$$

where

$$Q_\alpha = \frac{1}{2}\mathbf{p}^t\mathbf{\Delta}\mathbf{p} + \frac{1}{2}\mathbf{q}^t\mathbf{\Delta}\mathbf{q}$$

and

$$Q_\gamma = \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)^t \mathbf{\Delta} \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)$$

We have shown above that

$$Q_\gamma/T - Q_\alpha/T = \frac{1}{4}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{4}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q} - \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}$$

In addition,

$$1 - Q_\gamma/T = 1 - \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)^t (\mathbf{1}\mathbf{1}^t - \mathbf{\Sigma}) \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)$$

$$1 - Q_\gamma/T = \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)^t \mathbf{\Sigma} \left(\frac{\mathbf{p}+\mathbf{q}}{2}\right)$$

$$1 - Q_\gamma/T = \frac{1}{4}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{4}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q} + \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}$$

It follows that

$$1 - \frac{Q_\gamma - Q_\alpha}{(T - Q_\gamma)} = 1 - \frac{\frac{1}{4}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{4}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q} - \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}}{\frac{1}{4}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{4}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q} + \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}}$$

$$1 - \frac{Q_\gamma - Q_\alpha}{(T - Q_\gamma)} = \frac{\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}}{\frac{1}{4}\mathbf{p}^t\mathbf{\Sigma}\mathbf{p} + \frac{1}{4}\mathbf{q}^t\mathbf{\Sigma}\mathbf{q} + \frac{1}{2}\mathbf{p}^t\mathbf{\Sigma}\mathbf{q}} = S_\beta$$

2 Appendix S2. How to calculate similarities among species

All indices of similarity between two communities defined in the main text require the definition of taxonomic, phylogenetic, and functional similarities among species. We suggest that, wherever possible, these similarities be calculated using coherent formulas.

Taxonomic trees can be obtained using the hierarchical structure of a taxonomy (species embedded within genera, themselves embedded within families, and so on). Different branch levels can be attributed to taxonomic trees (differences between taxonomic levels, Clarke & Warwick, 1999). When branch lengths have been defined, we suggest treating taxonomic and phylogenetic trees similarly (Ricotta et al., 2012). Taxonomic and phylogenetic similarities among species can be defined using formulas of the fourth column of Table 2 of the main text, by defining a=sum of branch lengths from the nearest common ancestor of the two species to the root of the tree, b=sum of branch lengths from the first species to this nearest common ancestor, c=sum of branch lengths from the second species to this nearest common ancestor. Note that ultrametric trees are by definition those for which b=c.

When functional similarities have to be considered a first solution would be to establish a functional dendrogram and to treat it the same way as taxonomic and phylogenetic tree (*e.g.*, Petchey & Gaston, 2002). It should be recalled however that establishing a dendrogram does not avoid the step of choosing a coefficient of functional distances among species and it adds the methodological choice of a clustering approach. In addition, when a few traits only are considered, especially quantitative traits, the dendrogram can distort the functional distances among species. We thus suggest other solutions below.

If species are characterized by a multichoice trait of, say, H attributes, a species can be associated with several of these attributes. Functional similarities among species can be determined using formulas of the fourth column of Table 2 of the main text, with the following definitions: a= number of attributes shared by the two compared species; b= number of attributes associated only with the first species; c= number of attributes associated only with the second species. In the special case where only one attribute is possible per species, then all indices of similarity so defined would lead to 0 if the species compared do not have the same attribute and 1 if they have.

If species are characterized by a compositional or by a fuzzy trait (Chevenet, Dolédec & Chessel, 1994), then the association between a species and an attribute of the trait is quantified. A compositional trait has, say, H attributes, and a species is associated with each of these attributes with a specified proportion. The proportions sum to 1 over all attributes. Fuzzy traits are those traits for which the affinity of a species for an attribute is roughly estimated by an expert according to finite affinities, in general ranging from 0=no affinity, through 1 (low affinity), and 2 (medium affinity), to 3 (high affinity). Then the affinities are transformed into proportions per species. The vectors of proportions of two species can be compared using formulas of column 2 in Table 2 of the main text.

Formulas of Table 2 of the main text cannot be used in a general manner with quantitative traits. An index of similarity that relies on quantitative data and that provides positive semi-definite similarities is that of Gower (1971). If species are characterized by a quantitative trait Y, then for all i, j, the similarity between species i and j is

$$\sigma_{ij} = 1 - \frac{|y_i - y_j|}{\max_{u,j} |y_u - y_v|}$$

If several traits are considered, the similarity between two species can be calculated for each trait. Then the average similarity between two species across all traits can be computed. The property of positive semi-definiteness for the similarities among species is conserved by the averaging process (Theorem 1 in the Appendix of Gower, 1971). The similarities among species can thus be calculated either with single traits or with sets of traits, even sets, including quantitative, nominal, multichoice, compositional, and fuzzy traits.

3 Appendix S3. Manual for R functions and examples of their use

3.1 Manual

The R scripts of all functions described below are available in Appendix S4.

The R function dsimcom calculates the coefficients $S_{Sokal-Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$, S_{Ochiai}, and S_β of similarities among communities. It has the following usage:

```
> dsimcom(df, Sigma = NULL, method = 1:5, option=c("relative", "absolute"))
```

The parameters are defined as follows:

Parameter	Explanation
df	Data frame or matrix with species as rows, communities as columns and non-negative values as entries.
Sigma	Matrix of similarities among species (species as rows and columns **in the same order as in df**; values in Sigma bounded between 0 and 1).
method	an integer (1, 2, 3, 4, 5) indicating which coefficient should be used: $S_{Sokal-Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$, S_{Ochiai}, or S_β, respectively.
option	a character. If option = relative, the columns of df are standardized into proportions that sum to 1. If option = absolute, raw values are retained in df.

The result is a matrix of pair-wise similarities among communities.

Function SQ calculates index S_Q. It has the following usage:

```
> SQ(df, Sigma = NULL)
```

The parameters are defined as follows:

Parameter	Explanation
df	Data frame or matrix with species as rows, communities as columns and non-negative values as entries.
Sigma	Matrix of similarities among species (species as rows and columns **in the same order as in df**; values in Sigma bounded between 0 and 1).

The result is a matrix of pair-wise similarities among communities.

The functions simTaxphy and simTaxPhyBIS calculate (taxonomic or) phylogenetic similarities among species. They have the following usage:

```
> simTaxPhy(tree, method = c(1, 2, 3, 4, 5))
> simTaxPhyBIS(tree, method = c(1, 2, 3, 4, 5), rootedge = NULL)
```

The parameters are defined as follows:

Parameter	Explanation
tree	with simTaxPhy, tree is an object of class phylog in package ade4. With simTaxPhyBIS, tree is an object of class phylo in package ape.
method	an integer (1, 2, 3, 4, 5) indicating which coefficient should be used. see details below.
rootedge	a numeric equal to the length of the branch at the nearest common ancestor of all species, or for a taxonomy the nearest common taxonomic level (here referred to as the root node). This branch is thus anterior to the root. It is ignored if rootedge is null.

The result is a matrix of pair-wise similarities among species.

Details: Consider two species i and j. Let a be the sum of branch lengths between the nearest common ancestor (or common taxonomic level) of the two species and the root of the phylogenetic tree (or taxonomic tree). Let b be the sum of branch lengths between species i and this nearest common ancestor. Let c be the sum of branch lengths between species j and the nearest common ancestor. In simTaxPhy and simTaxPhyBIS, the similarity between the two species is:

- $a/(a+2b+2c)$ if method=1
- $a/(a+b+c)$ if method=2
- $2a/(2a+b+c)$ if method=3
- $a/\sqrt{(a+b)(a+c)}$ if method=4
- $4a/(4a+b+c)$ if method=5.

3.2 Example

First load the R scripts contained in Appendix S4.

An example of application is given below:

```
> library(ade4)
> data(macroloire) # data used in the main text
```

At first, similarities among communities are calculated by considering only the relative abundance of species within communities:

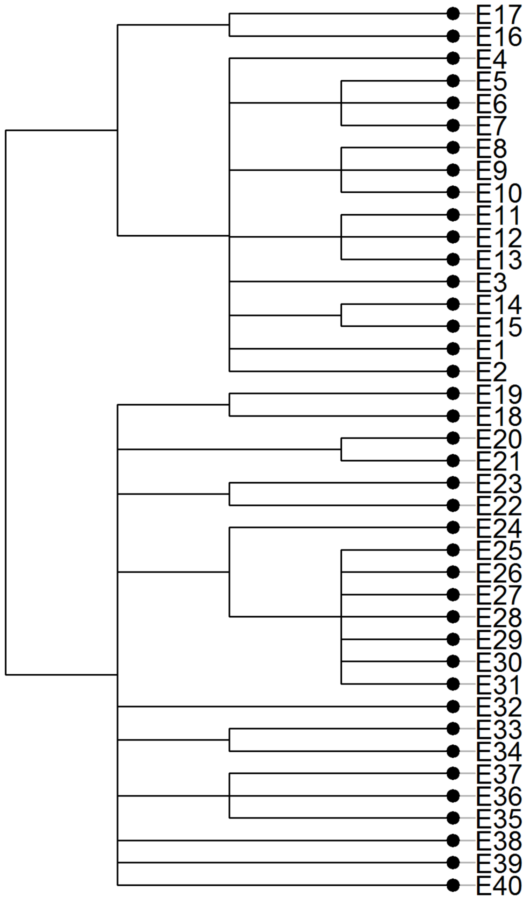
```
> Ssokalsneath <- dsimcom(macroloire$fau, method=1, option=c("relative"))
> Sjaccard <- dsimcom(macroloire$fau, method=2, option=c("relative"))
> Ssorensen <- dsimcom(macroloire$fau, method=3, option=c("relative"))
> Sochiai <- dsimcom(macroloire$fau, method=4, option=c("relative"))
> Sbeta <- dsimcom(macroloire$fau, method=5, option=c("relative"))
```

For comparison, the index S_Q is also calculated, considering only the relative abundance of species within communities.

```
> SQUNIF <- SQ(macroloire$fau)
```

Next, taxonomic similarities among species are added in the formulas:

```
> # The taxonomy is contained in macroloire$taxo
> # It is transformed into a tree with unit branch lengths
> # by the function taxo2phylog in package ade4
> # The resulting object is of class phylog.
> m.taxo <- taxo2phylog(macroloire$taxo, add.tools=TRUE)
> # Taxonomic tree
> plot(m.taxo)
```



Taxonomic similarities among species are computed using function simTaxPhy (see previous section):

```
> s_species_sokalsneath_taxo <- simTaxPhy(m.taxo, method=1) # Using formula a/(a+2b+2c)
> # (see notations below)
> s_species_jaccard_taxo <- simTaxPhy(m.taxo, method=2) # Using formula a/(a+b+c)
> s_species_sorensen_taxo <- simTaxPhy(m.taxo, method=3) # Using formula 2a/(2a+b+c)
> s_species_ochiai_taxo <- simTaxPhy(m.taxo, method=4) # Using a/sqrt((a+b)(a+c))
> s_species_beta_taxo <- simTaxPhy(m.taxo, method=5) # Using 4a/(4a+b+c)
```

a=sum of branch lengths from the nearest common ancestor of the two species to the root of the tree, b=sum of branch lengths from the first species to this nearest common ancestor, c=sum of branch lengths from the second species to this nearest common ancestor.

```
> # To check that these matrices of taxonomic similarities among species are p.s.d.
> # we have to verify that their eigenvalues are all nonnegative:
> all(eigen(s_species_sokalsneath_taxo)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_jaccard_taxo)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_sorensen_taxo)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_ochiai_taxo)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_beta_taxo)$val>-(1e-8))

[1] TRUE
```

Index S_Q requires Euclidean distances among species. For all indices s of similarity leading to p.s.d. matrices of pairwise similarities, $\sqrt{2(1-s)}$ has Euclidean properties. The calculation of S_Q can be done along with all matrices of taxonomic similarities among species defined above. Taxonomic similarities among communities can thus be computed as follows.

Scenario 1 with formulas related to Sokal & Sneath index:

```
> # Compositions of the communities
> m <- macroloire$fau[rownames(s_species_sokalsneath_taxo), ]
> # Taxomonic similarities among species
> s <- s_species_sokalsneath_taxo
```

Matrix of similarities among communities computed with index $S_{Sokal-Sneath}$

```
> Ssokalsneath_taxo <- dsimcom(m, s, method = 1)
```

Associated matrix of similarities among communities computed with index S_Q

```
> SQwith_species_sokalsneath_taxo <- SQ(m, s)
```

Scenario 2 with formulas related to Jaccard index:

```
> # Compositions of the communities
> m <- macroloire$fau[rownames(s_species_jaccard_taxo), ]
> # Taxonomic similarities among species
> s <- s_species_jaccard_taxo
```

Matrix of similarities among communities computed with index $S_{Jaccard}$

```
> Sjaccard_taxo <- dsimcom(m, s, method = 2)
```

Associated matrix of similarities among communities computed with index S_Q

```
> SQwith_species_jaccard_taxo <- SQ(m, s)
```

Scenario 3 with formulas related to Sørensen index:

```
> # Compositions of the communities
> m <- macroloire$fau[rownames(s_species_sorensen_taxo), ]
> # Taxonomic similarities among species
> s <- s_species_sorensen_taxo
```

Matrix of similarities among communities computed with index $S_{Srensen}$

```
> Ssorensen_taxo <- dsimcom(m, s, method = 3)
```

Associated matrix of similarities among communities computed with index S_Q

```
> SQwith_species_sorensen_taxo <- SQ(m, s)
```

Scenario 4 with formulas related to Ochiai index:

```
> # Compositions of the communities
> m <- macroloire$fau[rownames(s_species_ochiai_taxo), ]
> # Taxonomic similarities among species
> s <- s_species_ochiai_taxo
```

Matrix of similarities among communities computed with index S_{Ochiai}

```
> Sochiai_taxo <- dsimcom(m, s, method = 4)
```

Associated matrix of similarities among communities computed with index S_Q

```
> SQwith_species_ochiai_taxo <- SQ(m, s)
```

Scenario 5 with formulas related to S_β index:

```
> # Compositions of the communities
> m <- macroloire$fau[rownames(s_species_beta_taxo), ]
> # Taxonomic similarities among species
> s <- s_species_beta_taxo
```

Matrix of similarities among communities computed with index S_β

```
> Sbeta_taxo <- dsimcom(m, s, method = 5)
```

Associated matrix of similarities among communities computed with index S_Q

```
> SQwith_species_beta_taxo <- SQ(m, s)
```

Then, functional similarities among species are used in the formulas:

```
> # The matrix named feed below contains feeding attributes as rows,
> # species as columns, and affinities (proportions) as entries.
> feed <- t(macroloire$traits[ ,-(1:4)])
> rownames(feed)

[1] "Feed1" "Feed2" "Feed3" "Feed4" "Feed5" "Feed6" "Feed7"

> # Feeding habits comprise seven categories: engulfers, shredders, scrapers,
> # deposit-feeders, active filter-feeders, passive filter-feeders and piercers, in this order.
>
> # Functional similarities among species are computed as indicated in the main text
> s_species_sokalsneath_feed <- dsimcom(feed, method=1)
> s_species_jaccard_feed <- dsimcom(feed, method=2)
> s_species_sorensen_feed <- dsimcom(feed, method=3)
> s_species_ochiai_feed <- dsimcom(feed, method=4)
> s_species_beta_feed <- dsimcom(feed, method=5)
```

To check that these matrices of functional similarities among species are p.s.d., we have to verify that their eigenvalues are all nonnegative:

```
> all(eigen(s_species_sokalsneath_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_jaccard_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_sorensen_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_ochiai_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(s_species_beta_feed)$val>-(1e-8))

[1] FALSE
```

All are p.s.d. except s_species_beta_feed.

The functional similarities among communities can now be computed:

Scenario 1 with formulas related to Sokal-Sneath index:

```
> Ssokalsneath_feed <- dsimcom(macroloire$fau, s_species_sokalsneath_feed, method=1)
> SQwith_species_sokalsneath_feed <- SQ(macroloire$fau, s_species_sokalsneath_feed)
```

Scenario 2 with formulas related to Jaccard index:

```
> Sjaccard_feed <- dsimcom(macroloire$fau, s_species_jaccard_feed, method=2)
> SQwith_species_jaccard_feed <- SQ(macroloire$fau, s_species_jaccard_feed)
```

Scenario 3 with formulas related to Sørensen index:

```
> Ssorensen_feed <- dsimcom(macroloire$fau, s_species_sorensen_feed, method=3)
> SQwith_species_sorensen_feed <- SQ(macroloire$fau, s_species_sorensen_feed)
```

Scenario 4 with formulas related to Ochiai index:

```
> Sochiai_feed <- dsimcom(macroloire$fau, s_species_ochiai_feed, method=4)
> SQwith_species_ochiai_feed <- SQ(macroloire$fau, s_species_ochiai_feed)
```

The matrix named s_species_beta_feed is not p.s.d. The limits between 0 and 1 are thus not guarantied for index S_β applied to it.

S_β is thus applied below to s_species_sorensen_feed.

The similarities among communities and those among species are thus, in that case, computed with different mathematical formulas. Scenario 5 thus has formulas mixing S_β with species similarities related to Sørensen index:

```
> Sbeta_feed <- dsimcom(macroloire$fau, s_species_sorensen_feed, method=5)
```

Hereafter, matrix Sbeta_feed will thus be compared with matrix SQwithspecies_sorensen_feed (i.e. S_Q calculated from the functional interspecific similarities derived from Sørensen index).

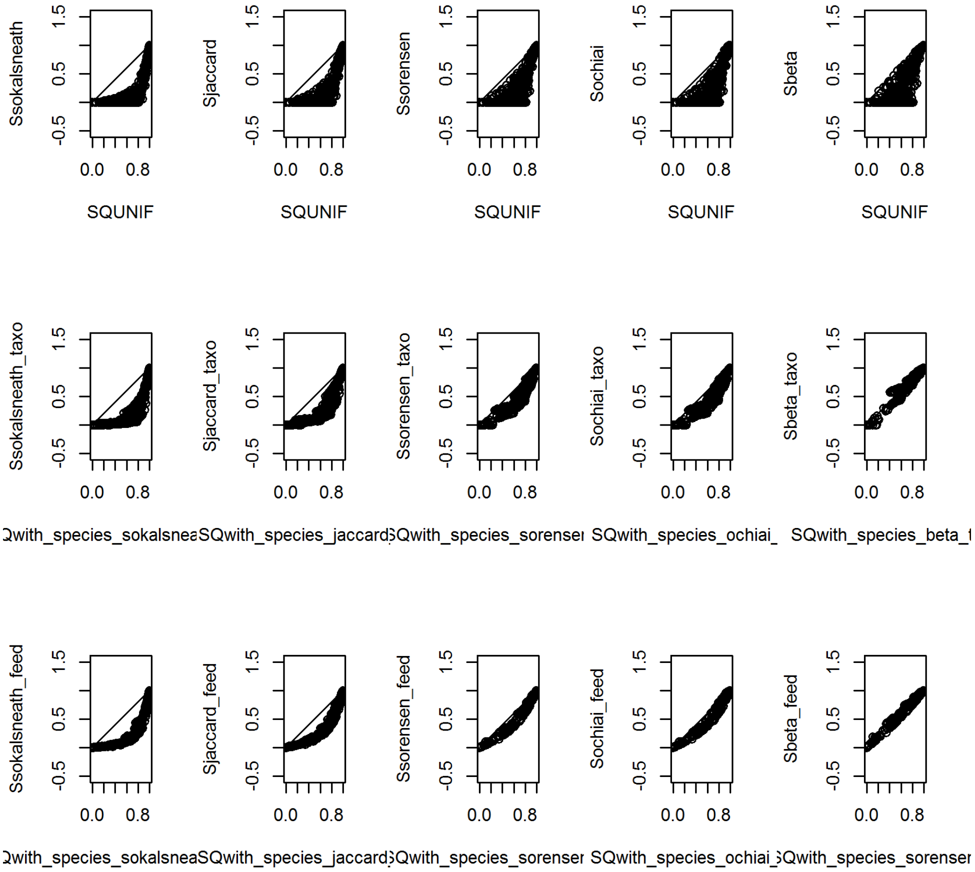
To check that these matrices of functional similarities among communities are p.s.d., we have to verify that their eigenvalues are all nonnegative:

```
> all(eigen(Ssokalsneath_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(Sjaccard_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(Ssorensen_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(Sochiai_feed)$val>-(1e-8))

[1] TRUE

> all(eigen(Sbeta_feed)$val>-(1e-8))

[1] FALSE
```

Even if applied to interspecific similarities that are p.s.d., the matrix Sbeta_feed is not p.s.d.

The differences between the values given by the new indices, those given by S_β, and those given by S_Q can be displayed as:

```
> par(mfrow=c(3, 5))
> plot(SQUNIF, Ssokalsneath, xlim=c(0,1), ylim=c(0,1), asp=1)
> segments(0, 0, 1,1)
> plot(SQUNIF, Sjaccard, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQUNIF, Ssorensen, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQUNIF, Sochiai, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQUNIF, Sbeta, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_sokalsneath_taxo, Ssokalsneath_taxo, xlim=c(0,1), ylim=c(0,1), asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_jaccard_taxo, Sjaccard_taxo, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_sorensen_taxo, Ssorensen_taxo, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_ochiai_taxo, Sochiai_taxo, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_beta_taxo, Sbeta_taxo, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_sokalsneath_feed, Ssokalsneath_feed, xlim=c(0,1), ylim=c(0,1), asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_jaccard_feed, Sjaccard_feed, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_sorensen_feed, Ssorensen_feed, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_ochiai_feed, Sochiai_feed, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
> plot(SQwith_species_sorensen_feed, Sbeta_feed, xlim=c(0,1), ylim=c(0,1) , asp=1)
> segments(0, 0, 1,1)
```



4 Appendix S4. R scripts for functions

A text file provides all functions introduced in Appendix S3.

5 Appendix S5. R scripts for examples

A text file provides all R scripts extracted from Appendix S3.

References

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```
dsimcom <- function(df, Sigma = NULL, method = 1:5, option=c("relative",
"absolute")){

    S <- Sigma
    if(!inherits(df, "data.frame"))
        df <- as.data.frame(df)
    if(is.null(S))
        S <- diag(rep(1, nrow(df)))
    S[S<0] <- 0
    S[S>1] <- 1
    method <- method[1]
    option <- option[1]
    if(option=="relative")
        dfp <- t(t(df)/colSums(df))
    else
        dfp <- as.matrix(df)
    fun2 <- function(df, S){
        A <- t(dfp)%*%S%*%dfp
        B <- matrix(1, ncol(dfp), ncol(dfp))%*%diag(diag(A))
        C <- diag(diag(A))%*%matrix(1, ncol(dfp), ncol(dfp))
        s <- A / (B+C-A)
        rownames(s)<-colnames(s)<-colnames(df)
        s[s<0]<-0
        s[s>1]<-1
        return(s)
    }
    fun1 <- function(df, S){
        A <- t(dfp)%*%S%*%dfp
        B <- matrix(1, ncol(dfp), ncol(dfp))%*%diag(diag(A))
        C <- diag(diag(A))%*%matrix(1, ncol(dfp), ncol(dfp))
        s <- A / (2*B+2*C-3*A)
        rownames(s)<-colnames(s)<-colnames(df)
        s[s<0]<-0
        s[s>1]<-1
        return(s)
    }
    fun3 <- function(df, S){
        A <- t(dfp)%*%S%*%dfp
        B <- matrix(1, ncol(dfp), ncol(dfp))%*%diag(diag(A))
        C <- diag(diag(A))%*%matrix(1, ncol(dfp), ncol(dfp))
        s <- 2*A / (B+C)
        rownames(s)<-colnames(s)<-colnames(df)
        s[s<0]<-0
        s[s>1]<-1
        return(s)
    }
    fun4 <- function(df, S){
        C <- t(dfp)%*%S%*%dfp
        W <- diag(1/sqrt(diag(C)))
        Scom <- W%*%C%*%W
        rownames(Scom)<-colnames(Scom)<-colnames(df)
        Scom[Scom<0]<-0
        Scom[Scom>1]<-1
        return(Scom)
    }
    fun5 <- function(df, S){
        A <- t(dfp)%*%S%*%dfp
        B <- matrix(1, ncol(dfp), ncol(dfp))%*%diag(diag(A))
        C <- diag(diag(A))%*%matrix(1, ncol(dfp), ncol(dfp))
        s <- 4*A / (2*A+B+C)
        rownames(s)<-colnames(s)<-colnames(df)
        s[s<0]<-0
        s[s>1]<-1
        return(s)
    }
    if(method == 1)
        return(fun1(df, S))
    if(method == 2)
        return(fun2(df, S))
    if(method == 3)
        return(fun3(df, S))
    if(method == 4)
        return(fun4(df, S))
    if(method == 5)
        return(fun5(df, S))
}

simTaxPhy <- function(tree, method = c(1, 2, 3, 4, 5)){

    # tree is an object of class phylog in ade4
    method <- method[1]
    a <- tree$Wmat
    ab <- diag(a)%*%t(rep(1, ncol(tree$Wmat)))
    ac <- rep(1, ncol(tree$Wmat))%*%t(diag(a))
    b <- ab-a
    c <- ac-a

    # similarities among species
    if (method==1)
    return(a/(a+2*b+2*c))
    if (method==2)
    return(a/(a+b+c))
    if (method==3)
    return(2*a/(2*a+b+c))
    if (method==4)
    return(a/sqrt((a+b)*(a+c)))
    if (method==5)
    return(4*a/(4*a+b+c))

}

simTaxPhyBIS <- function(tree, method = c(1, 2, 3, 4, 5),
rootedge = NULL){

    # tree is an object of class phylo in ape or adephylo
    method <- method[1]
    a <- vcv(tree)
    if(!is.null(rootedge))
    a <- a + rootedge
    ab <- diag(a)%*%t(rep(1, ncol(vcv(tree))))
    ac <- rep(1, ncol(vcv(tree)))%*%t(diag(a))
    b <- ab-a
    c <- ac-a

    # taxonomic similarities among species
    if (method==1)
    return(a/(a+2*b+2*c))
    if (method==2)
    return(a/(a+b+c))
    if (method==3)
    return(2*a/(2*a+b+c))
    if (method==4)
    return(a/sqrt((a+b)*(a+c)))
    if (method==5)
    return(4*a/(4*a+b+c))

}

SQ <- function(df, Sigma = NULL){

    if (!is.null(Sigma)){
    return(1-as.matrix(disc(as.data.frame(df),         as.dist(sqrt(2*(1-
Sigma)))))^2/2) }
    else
    return(1-as.matrix(disc(as.data.frame(df)))^2/2)
    # Function disc is available in library ade4

}
```

```
### R code from vignette source 'Suppl_PavoineRicotta.Rnw'
### Encoding: ISO8859-1

###################################################
### code chunk number 1: Suppl_PavoineRicotta.Rnw:64-68
###################################################
owidth <- getOption("width")
options("width"=80)
ow <- getOption("warn")
options("warn"=-1)


###################################################
### code chunk number 2: Suppl_PavoineRicotta.Rnw:354-355 (eval = FALSE)
###################################################
## dsimcom(df, Sigma = NULL, method = 1:5, option=c("relative",
"absolute"))


###################################################
### code chunk number 3: Suppl_PavoineRicotta.Rnw:379-380 (eval = FALSE)
###################################################
## SQ(df, Sigma = NULL)


###################################################
### code chunk number 4: Suppl_PavoineRicotta.Rnw:400-402 (eval = FALSE)
###################################################
## simTaxPhy(tree, method = c(1, 2, 3, 4, 5))
## simTaxPhyBIS(tree, method = c(1, 2, 3, 4, 5), rootedge = NULL)


###################################################
### code chunk number 5: Suppl_PavoineRicotta.Rnw:441-442
###################################################
source("AppendixS4.txt")


###################################################
### code chunk number 6: Suppl_PavoineRicotta.Rnw:447-449
###################################################
library(ade4)
data(macroloire) # data used in the main text


###################################################
### code chunk number 7: Suppl_PavoineRicotta.Rnw:453-458
###################################################
Ssokalsneath <- dsimcom(macroloire$fau, method=1, option=c("relative"))
Sjaccard <- dsimcom(macroloire$fau, method=2, option=c("relative"))
Ssorensen <- dsimcom(macroloire$fau, method=3, option=c("relative"))
Sochiai <- dsimcom(macroloire$fau, method=4, option=c("relative"))
Sbeta <- dsimcom(macroloire$fau, method=5, option=c("relative"))


###################################################
### code chunk number 8: Suppl_PavoineRicotta.Rnw:462-463
###################################################
SQUNIF <- SQ(macroloire$fau)
```

```
###################################################
### code chunk number 9: Suppl_PavoineRicotta.Rnw:467-474
###################################################
# The taxonomy is contained in macroloire$taxo
# It is transformed into a tree with unit branch lengths
# by the function taxo2phylog in package ade4
# The resulting object is of class phylog.
m.taxo <- taxo2phylog(macroloire$taxo, add.tools=TRUE)
# Taxonomic tree
plot(m.taxo)


###################################################
### code chunk number 10: Suppl_PavoineRicotta.Rnw:478-484
###################################################
s_species_sokalsneath_taxo <- simTaxPhy(m.taxo, method=1) # Using formula
a/(a+2b+2c)
# (see notations below)
s_species_jaccard_taxo <- simTaxPhy(m.taxo, method=2) # Using formula
a/(a+b+c)
s_species_sorensen_taxo <- simTaxPhy(m.taxo, method=3) # Using formula
2a/(2a+b+c)
s_species_ochiai_taxo <- simTaxPhy(m.taxo, method=4) # Using
a/sqrt((a+b)(a+c))
s_species_beta_taxo <- simTaxPhy(m.taxo, method=5) # Using 4a/(4a+b+c)


###################################################
### code chunk number 11: Suppl_PavoineRicotta.Rnw:493-500
###################################################
# To check that these matrices of taxonomic similarities among species
are p.s.d.
# we have to verify that their eigenvalues are all nonnegative:
all(eigen(s_species_sokalsneath_taxo)$val>-(1e-8))
all(eigen(s_species_jaccard_taxo)$val>-(1e-8))
all(eigen(s_species_sorensen_taxo)$val>-(1e-8))
all(eigen(s_species_ochiai_taxo)$val>-(1e-8))
all(eigen(s_species_beta_taxo)$val>-(1e-8))


###################################################
### code chunk number 12: Suppl_PavoineRicotta.Rnw:513-517
###################################################
# Compositions of the communities
m <- macroloire$fau[rownames(s_species_sokalsneath_taxo), ]
# Taxomonic similarities among species
s <- s_species_sokalsneath_taxo


###################################################
### code chunk number 13: Suppl_PavoineRicotta.Rnw:521-522
###################################################
Ssokalsneath_taxo <- dsimcom(m, s, method = 1)


###################################################
### code chunk number 14: Suppl_PavoineRicotta.Rnw:525-526
###################################################
SQwith_species_sokalsneath_taxo <- SQ(m, s)
```

```
###################################################
### code chunk number 15: Suppl_PavoineRicotta.Rnw:531-535
###################################################
# Compositions of the communities
m <- macroloire$fau[rownames(s_species_jaccard_taxo), ]
# Taxonomic similarities among species
s <- s_species_jaccard_taxo


###################################################
### code chunk number 16: Suppl_PavoineRicotta.Rnw:539-540
###################################################
Sjaccard_taxo <- dsimcom(m, s, method = 2)


###################################################
### code chunk number 17: Suppl_PavoineRicotta.Rnw:543-544
###################################################
SQwith_species_jaccard_taxo <- SQ(m, s)


###################################################
### code chunk number 18: Suppl_PavoineRicotta.Rnw:549-553
###################################################
# Compositions of the communities
m <- macroloire$fau[rownames(s_species_sorensen_taxo), ]
# Taxonomic similarities among species
s <- s_species_sorensen_taxo


###################################################
### code chunk number 19: Suppl_PavoineRicotta.Rnw:557-558
###################################################
Ssorensen_taxo <- dsimcom(m, s, method = 3)


###################################################
### code chunk number 20: Suppl_PavoineRicotta.Rnw:561-562
###################################################
SQwith_species_sorensen_taxo <- SQ(m, s)


###################################################
### code chunk number 21: Suppl_PavoineRicotta.Rnw:567-571
###################################################
# Compositions of the communities
m <- macroloire$fau[rownames(s_species_ochiai_taxo), ]
# Taxonomic similarities among species
s <- s_species_ochiai_taxo


###################################################
### code chunk number 22: Suppl_PavoineRicotta.Rnw:575-576
###################################################
Sochiai_taxo <- dsimcom(m, s, method = 4)


###################################################
```

```
### code chunk number 23: Suppl_PavoineRicotta.Rnw:579-580
###################################################
SQwith_species_ochiai_taxo <- SQ(m, s)


###################################################
### code chunk number 24: Suppl_PavoineRicotta.Rnw:585-589
###################################################
# Compositions of the communities
m <- macroloire$fau[rownames(s_species_beta_taxo), ]
# Taxonomic similarities among species
s <- s_species_beta_taxo


###################################################
### code chunk number 25: Suppl_PavoineRicotta.Rnw:593-594
###################################################
Sbeta_taxo <- dsimcom(m, s, method = 5)


###################################################
### code chunk number 26: Suppl_PavoineRicotta.Rnw:597-598
###################################################
SQwith_species_beta_taxo <- SQ(m, s)


###################################################
### code chunk number 27: Suppl_PavoineRicotta.Rnw:602-616
###################################################
# The matrix named feed below contains feeding attributes as rows,
# species as columns, and affinities (proportions) as entries.
feed <- t(macroloire$traits[ ,-(1:4)])
rownames(feed)

# Feeding habits comprise seven categories: engulfers, shredders,
scrapers,
# deposit-feeders, active filter-feeders, passive filter-feeders and
piercers, in this order.

# Functional similarities among species are computed as indicated in the
main text
s_species_sokalsneath_feed <- dsimcom(feed, method=1)
s_species_jaccard_feed <- dsimcom(feed, method=2)
s_species_sorensen_feed <- dsimcom(feed, method=3)
s_species_ochiai_feed <- dsimcom(feed, method=4)
s_species_beta_feed <- dsimcom(feed, method=5)


###################################################
### code chunk number 28: Suppl_PavoineRicotta.Rnw:620-625
###################################################
all(eigen(s_species_sokalsneath_feed)$val>-(1e-8))
all(eigen(s_species_jaccard_feed)$val>-(1e-8))
all(eigen(s_species_sorensen_feed)$val>-(1e-8))
all(eigen(s_species_ochiai_feed)$val>-(1e-8))
all(eigen(s_species_beta_feed)$val>-(1e-8))


###################################################
### code chunk number 29: Suppl_PavoineRicotta.Rnw:634-636
```

```
###################################################
Ssokalsneath_feed <- dsimcom(macroloire$fau, s_species_sokalsneath_feed,
method=1)
SQwith_species_sokalsneath_feed <- SQ(macroloire$fau,
s_species_sokalsneath_feed)


###################################################
### code chunk number 30: Suppl_PavoineRicotta.Rnw:640-642
###################################################
Sjaccard_feed <- dsimcom(macroloire$fau, s_species_jaccard_feed,
method=2)
SQwith_species_jaccard_feed <- SQ(macroloire$fau, s_species_jaccard_feed)


###################################################
### code chunk number 31: Suppl_PavoineRicotta.Rnw:646-648
###################################################
Ssorensen_feed <- dsimcom(macroloire$fau, s_species_sorensen_feed,
method=3)
SQwith_species_sorensen_feed <- SQ(macroloire$fau,
s_species_sorensen_feed)


###################################################
### code chunk number 32: Suppl_PavoineRicotta.Rnw:652-654
###################################################
Sochiai_feed <- dsimcom(macroloire$fau, s_species_ochiai_feed, method=4)
SQwith_species_ochiai_feed <- SQ(macroloire$fau, s_species_ochiai_feed)


###################################################
### code chunk number 33: Suppl_PavoineRicotta.Rnw:663-664
###################################################
Sbeta_feed <- dsimcom(macroloire$fau, s_species_sorensen_feed, method=5)


###################################################
### code chunk number 34: Suppl_PavoineRicotta.Rnw:670-675
###################################################
all(eigen(Ssokalsneath_feed)$val>-(1e-8))
all(eigen(Sjaccard_feed)$val>-(1e-8))
all(eigen(Ssorensen_feed)$val>-(1e-8))
all(eigen(Sochiai_feed)$val>-(1e-8))
all(eigen(Sbeta_feed)$val>-(1e-8))


###################################################
### code chunk number 35: Suppl_PavoineRicotta.Rnw:681-714
###################################################
par(mfrow=c(3, 5))
plot(SQUNIF, Ssokalsneath, xlim=c(0,1), ylim=c(0,1), asp=1)
segments(0, 0, 1,1)
plot(SQUNIF, Sjaccard, xlim=c(0,1), ylim=c(0,1) , asp=1)
segments(0, 0, 1,1)
plot(SQUNIF, Ssorensen, xlim=c(0,1), ylim=c(0,1) , asp=1)
segments(0, 0, 1,1)
plot(SQUNIF, Sochiai, xlim=c(0,1), ylim=c(0,1) , asp=1)
segments(0, 0, 1,1)
plot(SQUNIF, Sbeta, xlim=c(0,1), ylim=c(0,1) , asp=1)
```

```
segments(0, 0, 1,1)

plot(SQwith_species_sokalsneath_taxo,   Ssokalsneath_taxo,   xlim=c(0,1),
ylim=c(0,1), asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_jaccard_taxo, Sjaccard_taxo, xlim=c(0,1), ylim=c(0,1)
, asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_sorensen_taxo,      Ssorensen_taxo,      xlim=c(0,1),
ylim=c(0,1) , asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_ochiai_taxo, Sochiai_taxo, xlim=c(0,1), ylim=c(0,1) ,
asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_beta_taxo,  Sbeta_taxo,  xlim=c(0,1),  ylim=c(0,1)  ,
asp=1)
segments(0, 0, 1,1)

plot(SQwith_species_sokalsneath_feed,   Ssokalsneath_feed,   xlim=c(0,1),
ylim=c(0,1), asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_jaccard_feed, Sjaccard_feed, xlim=c(0,1), ylim=c(0,1)
, asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_sorensen_feed,      Ssorensen_feed,      xlim=c(0,1),
ylim=c(0,1) , asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_ochiai_feed, Sochiai_feed, xlim=c(0,1), ylim=c(0,1) ,
asp=1)
segments(0, 0, 1,1)
plot(SQwith_species_sorensen_feed, Sbeta_feed, xlim=c(0,1), ylim=c(0,1) ,
asp=1)
segments(0, 0, 1,1)
```