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# Functional and phylogenetic similarity among communities

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Running head: Intercommunity similarity

## Summary

**1.** Ecological studies often rely on coefficients of intercommunity (dis)similarity to decipher effects of ecological, evolutionary, human-driven mechanisms on the composition of

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communities. Yet, two main criticisms have been leveled at (dis)similarity coefficients. First, few developments include information on species' abundances, and either phylogeny or functional traits. Second, some (dis)similarity coefficients fail to always provide maximum dissimilarity between two completely distinct communities, i.e. 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 *et al.* 2008; Ricotta & Szeidl 2009, Ives & Helmus 2010; Nipperess, Faith & Barton 2010; Chiu, Jost & Chao 2013). 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:

$$Q = \sum_{ij} p_i p_j \delta_{ij}$$

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 pair-wise (functional or phylogenetic) dissimilarities among all species $i$ and $j$. Given two 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:

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

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' quadratic entropy index computed from vector $(\mathbf{p}+\mathbf{q})/2$, Champely & Chessel 1995). 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 & 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, *i.e.* 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, *i.e.* $\sum_{ij} p_i q_j \delta_{ij}$, 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, are high. The main objective of this study is 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 & 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:

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

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:

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

where $\sigma_{ij} = 1 - \delta_{ij}$ for all $i$, $j$ is a measure of pair-wise (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 $\sigma_{ij}$, the relative abundance vectors **p** and **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 **x** and **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

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

is a generalization of an index proposed by Sokal & Sneath (1963) for 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 community that are absent from the first community). In this special case, the coefficient $S_{Sokal\text{-}Sneath}$ reduces to

$$\frac{a}{a+2b+2c}$$

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

Likewise, the index

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

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

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

is a generalization of the index $S_{st}$ introduced above. $S_{Sørensen}$ is also a generalization of the Dice-Sørensen index for 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 & Chao (2013; see Appendix S1, section 1.2). 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

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

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 $\mathbf{\Delta} = \left(\sqrt{1-\sigma_{ij}}\right)$ 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: $0 \leq S_{Sokal\text{-}Sneath} \leq S_{Jaccard} \leq S_{Sørensen} \leq S_{Ochiai} \leq 1$ (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 **x** = **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 *et al.* (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 $\delta_{ij}$ 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 by 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, geographic 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 & 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

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

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

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 & 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 & Szeidl framework, is to define $D_\beta=\hat{\gamma}/\hat{\alpha}-1$, which can be written as:

$$D_\beta=\frac{\frac{1}{2}\sum_{ij}p_iq_j\delta_{ij}-\frac{1}{4}\sum_{ij}p_ip_j\delta_{ij}-\frac{1}{4}\sum_{ij}q_iq_j\delta_{ij}}{1-\frac{1}{2}\sum_{ij}p_iq_j\delta_{ij}-\frac{1}{4}\sum_{ij}p_ip_j\delta_{ij}-\frac{1}{4}\sum_{ij}q_iq_j\delta_{ij}}$$

Because $D_\beta$ 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 $S_\beta$ simplifies to:

$$S_\beta=\frac{4\sum_{ij}p_iq_j\sigma_{ij}}{2\sum_{ij}p_iq_j\sigma_{ij}+\sum_{ij}p_ip_j\sigma_{ij}+\sum_{ij}q_iq_j\sigma_{ij}}$$

where $\sigma_{ij}$ = 1 - $\delta_{ij}$ for all $i$, $j$ are pair-wise (functional or phylogenetic) similarities among species. Formula $S_\beta$ thus combines $\sum_{ij}p_iq_j\sigma_{ij}$, $\sum_{ij}p_ip_j\sigma_{ij}$, and $\sum_{ij}q_iq_j\sigma_{ij}$ 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 $D_\beta$, $S_\beta=1-D_\beta$ 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 $S_\beta$ is equivalent to the phylo-regional-overlap index of Chiu, Jost & Chao (2013) 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 behavior of $S_\beta$ 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 $S_\beta$ 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 behavior 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 analyzed in Ivol et al. (1997) and Pavoine & 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-analyze an old data set but rather to show where the indices of similarity proposed in Table 2 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, $c$=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 permitted 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 $j$,

$\sigma_{ij} = \sum_k a_{ik}a_{jk} / (2\sum_k a_{ik}^2 + 2\sum_k a_{jk}^2 - 3\sum_k a_{ik}a_{jk})$

where $a_{ik}$ and $a_{jk}$ are the relative affinities of species $i$ and $j$ to the $k^{th}$ 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 behavior of $S_{Sokal\text{-}Sneath}$, $S_{Jaccard}$, $S_{Sørensen}$, and $S_{Ochiai}$ was analyzed 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 to the taxonomy in Fig. 2 included only 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.

## 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 behavior between 1-COMDIST and the other indices. A criticism that can be raised towards COMDIST (and thus 1-COMDIST, Webb *et al.* 2008) is that it would provide equal levels of dissimilarity between two identical communities as between two communities with distinct species. This unexpected behavior 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 behavior 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 & 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 $S_{Sørensen}$ 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); (*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 & 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 index) 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 artifacts (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 2013). On the contrary, Rao's $D_Q$ has been early 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 versus 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 & Knight (2005), Ferrier *et al.* (2007), Pavoine, Love & Bonsall (2009), Nipperess, Faith & Barton (2010), and Chiu, Jost & Chao (2013) 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 & 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 & Maron (2003) 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.

## Data accessibility

Data are available in the R package ade4 (R Development Core Team 2013; Chessel, Dufour & Thioulouse 2004). 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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## Supporting Information

**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

**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‡ |
| $S_{Sokal-Sneath}$ | $\frac{\sum_{ij} x_i z_j \sigma_{ij}}{2\sum_{ij} x_i x_j \sigma_{ij} + 2\sum_{ij} z_i z_j \sigma_{ij} - 3}$ | $\frac{\sum_{i} x_i z_i}{2\sum_{i} x_i^2 + 2\sum_{i} z_i^2 - 3}$ | | $\frac{a}{a+2b+2c}$ | Sokal & Sneath (1963) |
| $S_{Jaccard}$ | $\frac{\sum_{ij} x_i z_j \sigma_{ij}}{\sum_{ij} x_i x_j \sigma_{ij} + \sum_{ij} z_i z_j \sigma_{ij} - \sum_{ij}$ | $\frac{\sum_{i} x_i z_i}{\sum_{i} x_i^2 + \sum_{i} z_i^2 - \sum_{i}$ | Wishart (1969) | $\frac{a}{a+b+c}$ | Jaccard (1901) |
| $S_{Søren sen}$ | $\frac{\sum_{ij} x_i z_j \sigma_{ij}}{\frac{1}{2}\sum_{ij} x_i x_j \sigma_{ij} + \frac{1}{2}\sum_{ij} z_i z_j \sigma_{ij}}$ | $\frac{\sum_{i} x_i z_i}{\frac{1}{2}\sum_{i} x_i^2 + \frac{1}{2}\sum_{i} z_i^2}$ | Morisita (1959) Horn (1966) | $\frac{2a}{2a+b+c}$ | Dice (1945) 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: e.g. 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 $\sum_i x_i z_i \Big/ \sqrt{\sum_i x_i^2 \sum_i z_i^2}$ 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; $c$=number of species found in the second community only.

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

| | Similarity indices among communities ($S$) and among species ($\sigma$) | | | | | | |
|---|---|---|---|---|---|---|---|
| | $S_{Sokal\text{-}Sneath}$ | $S_Q$ calculated with $\sigma_{Sokal\text{-}Sneath}$ | $S_{\text{Jaccard}}$ | $S_Q$ 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, $c$ = 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.

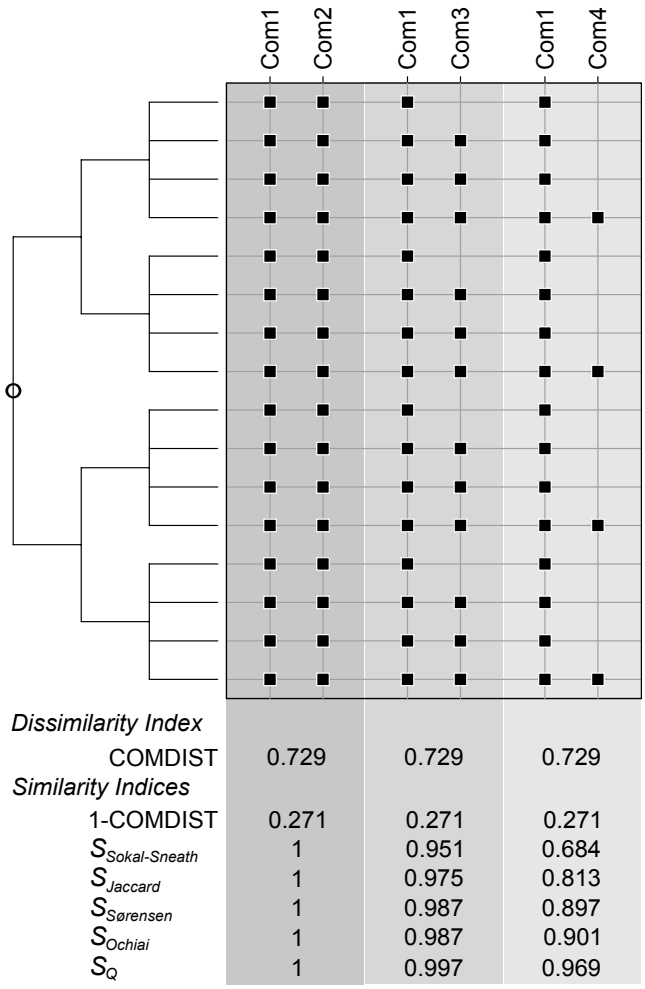
Figure Legends

**Fig. 1.** Behavior of COMDIST for a small data set composed of four communities (Com1 to 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 $i$th 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.

**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.

**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; (c) similarities in feeding habits. Spearman correlations between the new indices and $S_Q$ are indicated on each panel.




| | | | |
|---|---|---|---|
| *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 |