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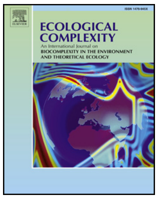

A family of (dis)similarity measures based on evenness and its relationship with beta diversity

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ABSTRACT

In this paper, I propose a new evenness-based method for calculating plot-to-plot (dis)similarity coefficients. The method is very flexible, as (dis)similarity can be calculated for any kind of species abundance data (also including functional or phylogenetic differences between species), and can be easily generalized to multiple sites. To show how the proposed method works in practice, the behavior of two similarity coefficients based on Pielou's and Williams' evenness is examined with simulated data representing an ideal ecological gradient. Being derived from classical evenness indices, which have been used in ecology for decades, this new family of measures has a great potential for future research in community ecology and multivariate analysis.

1. Introduction

Ecologists often rely on (dis)similarity or resemblance measures between pairs of plots to explore the effects of ecological, evolutionary or anthropogenic mechanisms on community assembly. Since ecological data are often multivariate of high complexity, literally dozens of such measures have been proposed to summarize various facets of plot-to-plot resemblance. Most of these measures are based either on species presences and absences within plots or on species abundance data. However, the importance of measures that incorporate information on interspecies differences is becoming increasingly recognized (Rao, 1982; Champely and Chessel, 2002; Nipperess et al., 2010; Chao et al., 2014; Pavoine and Ricotta, 2014). In addition, it has been recently observed that if resemblance measures are used in multiple-site studies for comparing the beta diversity of more than two plots, inference drawn from mean values may be misleading, because pairwise resemblance coefficients cannot account properly for co-occurrence patterns of species in many sites. Therefore, so-called multiple-site indices are required (Diserud and Ødegaard, 2007; Baselga et al., 2007; Arita, 2017).

In this paper, I propose a new family of plot-to-plot resemblance measures, which can be calculated either from species presence and absence data, or from absolute or relative species abundances. Being based on a weighted version of classical evenness indices, which have been used in ecology for decades, this new family of measures has a great potential for future research in community ecology. The paper is organized as follows: first, the new family of plot-to-plot resemblance coefficients is presented. Next, I show how to incorporate interspecies dissimilarities into the new measures and how to generalize these measures to calculate multiple-site resemblance or beta diversity. Finally, the behavior of the proposed family of measures is shown by graphical comparisons based on simulated data representing an ideal ecological gradient.

2. A new family of (dis)similarity measures

Biological diversity is a central concept in ecology for linking community structure to ecosystem functioning. Traditional biodiversity measures usually combine in non-standard way two components: the number of species and their relative abundance distribution (called variously evenness, equitability or dominance).

For one single plot containing K species with relative abundances p_j ($j = 1, 2, \ldots, K$) where $0 \leq p_j \leq 1$ and $\sum_{j=1}^{K} p_j = 1$, a measure of evenness E typically behaves such that its maximum value $\max E = 1$ is obtained for a perfectly even distribution in which all species have relative abundances $\bar{p}_j = 1/K$, and minimum evenness $\min E = 0$ is obtained if there is a species with relative abundance p_j approaching one (the abundances of all other species being close to zero).

While in ecology evenness measures have been traditionally used for summarizing the species equitability in one plot, here evenness is used to quantify the similarity in species composition between two plots. Take for example the classical Pielou evenness (Pielou, 1966) $E = H/\log K$, where H is the Shannon diversity $H = \sum_{j=1}^{K} p_j \log(1/p_j)$, and let m and n be two plots (or assemblages, communities, sites, quadrats, etc.) containing the abundance values x_{jm} and x_{jn} of species j in m and n, respectively. The quantities x_{jm} and x_{jn} can contain any non-

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negative value of choice, such as presence and absence data, absolute abundances (measured either as number of individuals, cover or biomass data), or relative abundances that sum to one over all species in a given plot.

First, the abundances x_{jm} and x_{jn} of species j in plots m and n are transformed to relative values $p_{jm} = x_{jm}/(x_{jm} + x_{jn})$ and $p_{jn} = x_{jn}/(x_{jm} + x_{jn})$ such that $p_{jm} + p_{jn} = 1$. Next, the evenness of species j is calculated as:

$$E_j = \frac{H_j}{\log N} = \frac{p_{jm}\log(1/p_{jm}) + p_{jn}\log(1/p_{jn})}{\log 2} \tag{1}$$

Finally, total plot-to-plot similarity S_{mn} is obtained as the weighted average of the single-species values E_j:

$$S_{mn} = \sum_{j=1}^{K} w_j \times E_j \tag{2}$$

The values of the species-specific weights w_j (with $0 \le w_j \le 1$ and $\sum_{j=1}^{K} w_j = 1$) may vary according to the particular context of the study. Dealing with species abundance data, the contribution of species j to overall plot-to-plot dissimilarity may be weighted by the pooled abundance of j in m and n such that: $w_j = (x_{jm} + x_{jn})/\sum_{j=1}^{K}(x_{jm} + x_{jn})$ where $\sum_{j=1}^{K}(x_{jm} + x_{jn})$ is the total abundance of all species in both plots. To the contrary, for species presence and absence data, all weights can be set equal to $1/K$. However, the values of the species-specific weights w_j may also take different values related to the species conservation value, their phylogenetic and/or functional originality, or to any other biological parameter that is thought to influence ecosystem functioning at the plot scale.

For one single species, $E_j = 0$ if the species is present only in one plot such that $p_{jm} = 1$ and $p_{jn} = 0$, while $E_j = 1$ if the species is present in both plots with the same relative abundance $p_{jm} = p_{jn} = 0.5$. If all weights $w_j > 0$, $S_{mn} = 1$ if and only if m and n are identical, and $S_{mn} = 0$ if both plots do not share any common species. Starting from Eq. (2), an associated plot-to-plot dissimilarity coefficient D_{mn} can be simply calculated as:

$$D_{mn} = 1 - S_{mn} = \sum_{j=1}^{K} w_j \times D_j \tag{3}$$

with $D_j = (1 - E_j)$. Note that in principle it would be possible to use directly the Shannon diversity (or any other suitable diversity measure) instead of evenness for calculating the similarity between two plots. With most indices of evenness being basically normalized diversity measures bounded in the range (0–1), there is no fundamental difference between diversity and evenness when diversity comparisons are restricted to a fixed number of plots. However, being bounded in the range (0–1), thereby controlling for the number of plots, evenness measures allow to generalize similarity coefficients to multiple sites (see below).

Eqs. (2) and (3) are both expressed as a weighted average of single-species values. Therefore, S_{mn} and D_{mn} can be additively decomposed into the contribution of their constituting elements $w_j \times E_j$ and $w_j \times D_j$, thus enabling to determine the relevance of single species to overall (dis)similarity. Ricotta (2017) further showed that for species presence and absence data, if plot-to-plot dissimilarity is calculated with equal weights $w_j = 1/K$ for all species, D_{mn} is equal to the Jaccard dissimilarity, while setting the weights w_j proportional to the number of species presences in both plots, D_{mn} is equal to the Sørensen dissimilarity. This relationship reinforces the interpretation of S_{mn} and D_{mn} as resemblance measures.

3. Including interspecies resemblances in evenness-based (dis)similarity

In the previous section, I defined a new family of plot-to-plot resemblance measures based on any kind of abundance data; here, I show how to incorporate information on the extent of interspecies differences into these measures. Such differences can be based either on phylogenetic or functional relationships among species, as both of them are believed to reflect ecological processes (Nipperess et al., 2010; Chiu et al., 2014; Pavoine and Ricotta, 2014).

Interspecies differences are generally summarized by a square matrix of $K \times K$ species with functional or phylogenetic dissimilarities δ_{ij} between species i and j with $\delta_{ij} = \delta_{ji}$ and $\delta_{ii} = 0$. If δ_{ij} is in the range (0–1), a corresponding similarity coefficient σ_{ij} can be simply obtained as $\sigma_{ij} = 1 - \delta_{ij}$. Note that every dissimilarity measure with an upper bound $\max\delta > 1$ can be normalized in the range (0–1) dividing each term by $\max\delta$, while dissimilarity measures that do not possess an upper bound, such as phylogenetic distances, can be locally normalized in the range (0–1) by dividing each term δ_{ij} by the maximum value found in the data set (Ricotta and Pavoine, 2015a).

Leinster and Cobbold (2012) defined the abundance of species similar to j in plot n as:

$$z_{jn} = \sum_{i=1}^{K} x_{in} \times \sigma_{ij} \tag{4}$$

where the sum in Eq. (4) is over all species with non-zero abundance in at least one of the two plots m and n (i.e. the species for which $x_{jm} + x_{jn} > 0$). According to Eq. (4), the abundance of all species similar to j (including j itself) is always higher than the abundance of j (i.e. $x_{jn} \le z_{jn} \le \sum_{j=1}^{K} x_{jn}$, where $\sum_{j=1}^{K} x_{jn}$ is the total species abundance in plot n). z_{jn} is large if most species in n are functionally (or phylogenetically) similar to j. To the contrary, if j is a functionally unique species, we have $z_{jn} \approx x_{jn}$ (Ricotta et al., 2016). Accordingly, for a given species j, the quantity z_{jn} summarizes the commonness of all individuals in plot n that support to some extent the functions associated with j. Leinster and Cobbold (2012) defined z_{jn} as the ordinariness of species j.

Based on the notion of species ordinariness, we can extend the proposed family of resemblance measures to include phylogenetic or functional relationships among species. This can be done by simply substituting the species abundances x_{jn} with the quantities z_{jn} in the calculation of S_{mn} or D_{mn}, thus providing a very general framework for summarizing species turnover between two plots.

4. Extending evenness-based (dis)similarity to multiple sites

Multiple-site resemblance is closely related to the concept of beta diversity proposed by Whittaker (1960) to define the amount of variation in species composition among sampling units. While evaluation of multiple-site resemblance is commonly based on the average (dis)similarity between pairs of plots (Izsák and Price, 2001; Koleff et al., 2003), this approach ignores the information on the number of species shared among more than two plots. To get insight on the identity of species shared across more than two plots, multiple-site resemblance measures are needed (Diserud and Ødegaard, 2007; Baselga et al., 2007; Chao et al., 2012; Ricotta and Pavoine, 2015b).

To extend evenness-based resemblance to multiple sites, let $\mathbf{X}$ be a rectangular community composition matrix containing the abundances x_{jn} of K species (rows $j = 1, 2, \ldots, K$) in N plots (columns $n = 1, 2, \ldots, N$). First, the absolute abundances x_{jn} of j are transformed to relative values $p_{jn} = x_{jn}/x_{j+}$ by dividing them by the row sum $x_{j+} = \sum_{n=1}^{N} x_{jn}$. Next, Pielou's evenness of species j is calculated as:

$$E_j = \frac{H_j}{\log N} = \frac{\sum_{n=1}^{N} p_{jn}\log(1/p_{jn})}{\log N} \tag{5}$$

Finally, like for the two-plot case, overall multiple-site similarity S obtained as the weighted average of the evenness values of single-species:

$$S = \sum_{j=1}^{K} w_j \times E_j \tag{6}$$

where w_j is any weighting factor associated to species j. As usual, the associated multiple-site dissimilarity coefficient D or beta diversity of the entire community composition matrix can be calculated as $D = 1 - S$. This definition reduces plot-to-plot resemblance to a special case of more general multiple-site coefficients. Ricotta (2017) observed that if multiple-site dissimilarity or beta diversity is calculated with Pielou's evenness and the weights of single species are set proportional to their abundances such that $w_j = x_{j+}/x_{++}$ (where $x_{++} = \sum_{n=1}^{N} \sum_{j=1}^{K} x_{jn}$ is the total species abundance in $\mathbf{X}$), D becomes equal to the mutual information measure proposed by Chao and Chiu (2016, Eq. (11c)) to link traditional diversity decomposition into alpha, beta and gamma components to the variance of the community composition matrix. For details, see Chao and Chiu (2016).

5. Worked example

Although the main purpose of this paper is to provide a first theoretical treatment of evenness-based resemblance, the behavior of the proposed coefficients was investigated by graphical evaluation of artificial plant communities along a simulated gradient. To this end, I used the community composition matrix in Ricotta and Pavoine (2015a), together with the associated species dissimilarity matrix. The community composition matrix contains the artificial abundances of 15 species in 9 plots (Table 1). All species show an unimodal response to a simulated one-dimensional gradient with varying length and abundance. The dissimilarity matrix (available in Ricotta and Pavoine, 2015a, Appendix S2) was generated such that the observed dissimilarities between species pairs reflect their ecological differences along the gradient.

To highlight the effects of species turnover on evenness-based resemblance, I used conventional profile diagrams (see e.g. Podani, 2000). I calculated the evenness-based similarity of the first plot with itself and with all other plots in $\mathbf{X}$. The graph of the resulting values shows how changes in community composition affect changes in plot-to-plot similarity along the simulated gradient.

Plot-to-plot similarity S in Eq. (6) was calculated with two classical measures of evenness: Pielou's evenness (Eq. (5)), which is by far the most popular measure of evenness in ecology (Jost, 2010; Kvålseth, 2015), and the index of Williams (Engen, 1979):

$$E_j = 1 - \left[\left(N \sum_{n=1}^{N} p_{jn}^2 - 1 \right) / (N - 1) \right]^{\frac{1}{2}} \tag{7}$$

Table 1
Artificial data matrix with the abundances of 15 species (S1–S15) in 9 Plots (P1–P9) ordered along a simulated ecological gradient with unimodal species responses of varying length and abundance.

Species	Plots								
	P1	P2	P3	P4	P5	P6	P7	P8	P9
S1	2	1	·	·	·	·	·	·	·
S2	2	1	·	·	·	·	·	·	·
S3	3	2	1	·	·	·	·	·	·
S4	4	3	2	1	·	·	·	·	·
S5	·	1	·	·	·	·	·	·	·
S6	·	·	1	·	·	·	·	·	·
S7	2	3	4	3	2	1	·	·	·
S8	·	1	2	3	2	1	·	·	·
S9	1	2	3	4	3	2	1	·	·
S10	·	·	·	1	2	1	·	·	·
S11	·	·	·	·	·	1	·	·	·
S12	·	·	·	·	·	·	1	2	1
S13	·	·	·	·	1	2	3	4	5
S14	·	·	·	·	·	·	1	2	3
S15	·	·	·	·	·	·	·	1	2

The reason for this choice will be clear in the next section. For each similarity index, I calculated the abundance-based version of S, together with its functional analogue based on the quantities z_{jn} (the functional ordinariness of species j defined in Eq. (4)). In all cases, the species weights w_j were set proportional to the species abundances in both plots.

The profile diagrams of the abundance-based and the functional versions of the Pielou and the Williams similarity are shown in Fig. 1. Both abundance-based measures show a decreasing pattern that mirrors the species turnover along the simulated gradient. As expected, for both abundance-based measures, maximal similarity $S = 1$ is obtained comparing plot P1 with itself, whereas minimal similarity $S = 0$ is obtained comparing P1 with P8 and P9, which do not have any species in common with P1. The same decreasing pattern, although with a different profile shape, is shown by the functional versions of the similarity measures. In this latter case, the species are expected to share some degree of ecological functioning. Therefore, the resulting plot-to-plot functional similarity values are systematically higher than the corresponding abundance-based values.

6. Discussion

This paper introduces a new framework for calculating the (dis)similarity between a pair of plots. From an operational viewpoint, the profile diagrams in Fig. 1 show that evenness-based measures are reasonably able to reflect the species sorting along the simulated gradient. Note that an R script for calculating plot-to-plot (dis)similarity with Pielou's evenness can be found in Ricotta (2017, Appendix 1). More generally, the method is very flexible, as (dis)similarity can be calculated for any kind of species abundance data (including functional or phylogenetic differences between species) and can be smoothly generalized to multiple sites. This high flexibility in the selection of the appropriate evenness measure, weighting factor and abundance data is very useful, as there is no single ideal measure that is able to summarize all aspects of plot-to-plot similarity (Pavoine and Ricotta, 2014). At the same time, due to the many combinations of measures, weighting factors and abundance data, a more detailed comparison of the new family of evenness-based measures with other 'standard' dissimilarity indices, as is usually done in more applied contexts, would be necessarily reductive. To use the proposed measures in practice, the researcher will have to select case by case among the many available options the most suitable ones for answering his/her specific questions.

Many authors (Hill, 1973; Engen, 1979; Taillie, 1979; Routledge, 1983; Smith and Wilson, 1996; Ricotta, 2003; Jost, 2010; Tuomisto, 2012; Kvålseth, 2015) have proposed a number of properties that an evenness index should meet to reasonably behave in ecological research. However, there is no single index that can satisfy even a basic set of them (Routledge, 1983). With a focus on index properties, Kvålseth (2015) introduced the so-called 'value-validity property'. This essentially requires that an evenness index E provides a realistic representation of the distance of the actual species abundance distribution under scrutiny from the extreme distributions $P_0 = (1, 0, \ldots, 0)$ and $P_1 = (1/N, \ldots, 1/N)$ for which E is expected to assume its minimum and maximum values.

Let P_j be the distribution of the relative abundances of species j in N plots: $P_j = (p_{j1}, p_{j2}, \ldots, p_{jN})$. Kvålseth (2015, Eq. (19)) observed that the index of Williams can be expressed as the complement of the Euclidean distance d between P_j and P_1 normalized by the distance between the extreme distributions P_0 and P_1:

$$E_j = 1 - \frac{d(P_j, P_1)}{d(P_0, P_1)} \tag{8}$$

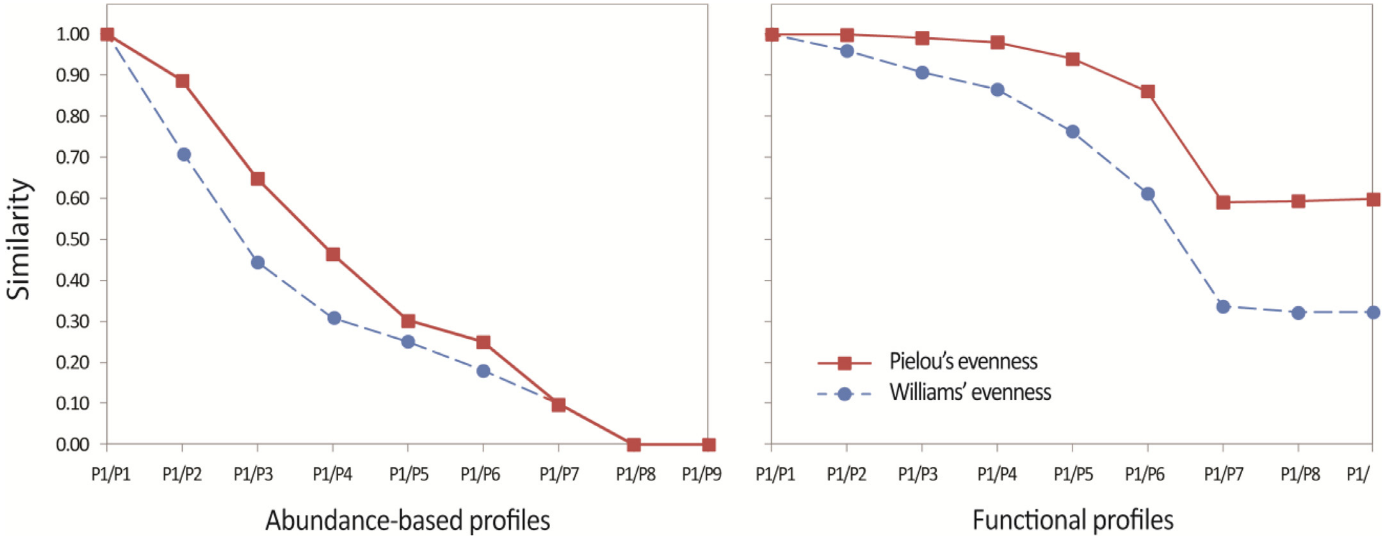

Fig. 1. Profile diagrams showing the response of the similarity coefficients to the simulated ecological gradient in Table 1. Plot P1 is compared to itself and to all other plots in Table 1.

Being based on Euclidean distances between relevant species abundance distributions, the index of Williams automatically conforms to the value-validity property throughout its range. For details, see Kvålseth (2015). To the contrary, the index of Pielou tends to systematically overestimate evenness (Molinari, 1989; Bulla, 1994), thus leading to overestimated plot-to-plot similarity, as shown by the profile diagrams in Fig. 1.

The lack of the value-validity property makes the conversion of the index values to a qualitative scale, such as low, medium, high, or very high impossible, so that for the Pielou evenness only the ordering of values (a is larger than b) conveys meaningful information (Ricotta and Pavoine, 2015a). At the same time, the observation that the index of Williams can be expressed in terms of normalized distances between abundance distributions leads us to interpret Pielou's index in a similar fashion.

Let $P = (p_1, p_2, ..., p_N)$ and $Q = (q_1, q_2, ..., q_N)$ be two relative abundance distributions that are in some way connected to each other. Shannon (1948) proved that $\sum_{n=1}^{N} p_n \log(1/p_n) \le \sum_{n=1}^{N} p_n \log(1/q_n)$ where the quantity

$$H(P\|Q) = \sum_{n=1}^{N} p_n \log(p_n/q_n) = \sum_{n=1}^{N} p_n \log(1/q_n) - \sum_{n=1}^{N} p_n \log(1/p_n) \tag{9}$$

is an asymmetric measure of information-theoretical dissimilarity between P and Q, also known as information gain or Kullback's (1959) divergence.

$H(P\|Q)$ is defined only if $q_n > 0$ and if there is a one-to-one correspondence between the elements of P and Q. Although some elements of the summation $\sum_{n=1}^{N} p_n \log(p_n/q_n)$ may be negative, $H(P\|Q)$ is always non-negative with $0 \le H(P\|Q) \le \log N$.

$H(P\|Q)$ thus provides an asymmetric measure of how much two distributions differ. Therefore, we can use the information gain to examine the divergence of an observed distribution from a theoretical reference distribution. In this view, the quantity $H(P\|P_1)$ where P_1 is a perfectly even distribution in which all objects have relative abundances $\overline{p}_n = 1/N$, provides an adequate measure of departure of the observed distribution P from perfect evenness (Feldman and Crutchfield, 1998; Chao and Chiu, 2016).

A little algebra shows that $\sum_{n=1}^{N} p_n \log(p_n/\overline{p}_n) = \log N - \sum_{n=1}^{N} p_n \log(1/p_n)$, which is the usual notation for Theil's (1967) inequality measure used in econometrics for summarizing the distribution of household incomes. Accordingly, Pielou's multiple-site dissimilarity D or beta diversity can be reformulated as a weighted average of the normalized divergences of single species from a perfectly even distribution:

$$D = \sum_{j=1}^{K} w_j \times \left(1 - \frac{H_j}{\log N}\right) = \sum_{j=1}^{K} w_j \times \left(\frac{\log N - \sum_{n=1}^{N} p_{jn} \log(1/p_{jn})}{\log N}\right) \tag{10}$$

where the ratio

$$D_j = \frac{\log N - \sum_{n=1}^{N} p_{jn} \log(1/p_{jn})}{\log N} = \frac{H(P_j\|P_1)}{\max H(P_j\|P_1)} \tag{11}$$

represents the divergence between the observed abundance distribution of species j and the reference distribution P_1 normalized by its maximum value (Kvålseth, 2015).

Eq. (10) thus shows that Pielou's evenness can also be interpreted as a normalized distance between relevant species abundance distributions. This distance-based interpretation of evenness raises the questions: can we express other classical evenness measures in the same way? Among the many available multivariate dissimilarity measures (Podani, 2000; Legendre and Legendre, 2012), which ones can be used to get an appropriate multiple-site beta diversity expressed as $D = \sum_{j=1}^{K} w_j \times d(P_j, P_1)/d(P_0, P_1)$? These are critical questions and their answer may provide valuable insights on the relationships between (dis)similarity, evenness and beta diversity.

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