



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 ($j = 1, 2, \dots, K$) 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:

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

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

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

The values of the species-specific weights w_j (with $0 \leq w_j \leq 1$ 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:

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

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:

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

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. $x_{jn} \leq z_{jn} \leq \sum_{j=1}^K x_{jn}$, 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 $j = 1, 2, \dots, K$) in N plots (columns $n = 1, 2, \dots, N$). 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:

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

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

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