



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



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ABSTRACT

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

1. Introduction

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

More recently, a number of 'functional dissimilarity measures' have been proposed for summarizing different facets of functional differences among plots (Rao, 1982; Clarke and Warwick, 1998; Izsák and Price, 2001; Champely and Chessel, 2002; Pavoine et al., 2004; Chiu et al., 2014; Pavoine and Ricotta, 2014; Ricotta et al., 2016). Such new dissimilarity measures incorporate information on the species functional traits. Therefore, they are expected to correlate more strongly

with ecosystem-level processes, as species influence these processes via their traits (Mason and de Bello, 2013). Since functional dissimilarity measures have been developed for capturing new aspects of ecological differences among plots, they are usually not directly related to more traditional measures of species turnover which are based solely on species incidence or abundance data.

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

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2. Methods

2.1. A general family of traditional dissimilarity measures

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

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

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

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

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

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

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

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

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

where

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

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

As shown by Eq. (4), the Bray-Curtis dissimilarity can be expressed as a normalized form of the Canberra distance in which the contribution of species j to overall dissimilarity $|x_{Uj} - x_{Vj}| / (x_{Uj} + x_{Vj})$ is weighted by the relative abundance of j in plots U and V . Based on the observed relationship between the Bray-Curtis dissimilarity and the normalized Canberra distance, Ricotta and Podani (2017) defined a ‘generalized Canberra dissimilarity’ which includes BC and NC as special cases:

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

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

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

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

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

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

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

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

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

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

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

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

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

2.2. A new family of functional dissimilarity measures

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

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

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

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

Given two functionally identical plots U and V , we have that for each species in U and V , the ordinariness $z_{Uj} = \sum_{i=1}^N x_{Ui} \sigma_{ij}$ in plot U is equal to the corresponding value $z_{Vj} = \sum_{i=1}^N x_{Vi} \sigma_{ij}$ in plot V . In other words, for two functionally identical plots, the abundance of the species similar to j in plot U is equal to the abundance of the species similar to j in plot V (for definitions and proofs see Appendix 1). In contrast, for two maximally distinct assemblages, either z_{Uj} or z_{Vj} is equal to zero, meaning that the species in plot U do not have any functional analogue in plot V .

Hence, in principle, we could calculate a measure of functional dissimilarity among plots with any of the many traditional dissimilarity measures developed for species abundance data by simply replacing the species abundances x_{Uj} and x_{Vj} in both plots with their corresponding species ordinariness z_{Uj} and z_{Vj} . The resulting measures meet the foremost requirements for a dissimilarity coefficient in the range [0, 1]: for two maximally dissimilar plots (i.e. two plots with no species in

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