



Short Note

On some properties of the Bray-Curtis dissimilarity and their ecological meaning

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ABSTRACT

In this paper, we examine some basic properties of the Bray-Curtis dissimilarity as compared with other distance and dissimilarity functions applied to ecological abundance data. We argue that the ability of every coefficient to measure species-level contributions is a fundamental requirement. By suggesting an additive decomposition formula for the Bray-Curtis coefficient we derive a general formula of dissimilarity, which includes the Canberra distance and the Bray-Curtis dissimilarity as special cases. A similar general formula is also proposed for the Marczewski-Steinhaus coefficient. Finally, using a modified version of Dalton's principle of transfers, we show that the Bray-Curtis coefficient and the city-block distance exhibit a linear response to the transfer of species abundances from an abundant plot to a less abundant plot. At the other extreme, the chord and the Hellinger distances show an irregular and non-monotonic behavior.

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1. Introduction

Ecologists routinely use dissimilarity measures **between pairs** of plots (or species assemblages, communities, sites, quadrats, etc.) to explore community assembly processes. Given two plots U and V , a logical starting point for evaluating any other dissimilarity measure is the Euclidean distance because it corresponds to our everyday feeling about interpoint distances in the visible and easily measurable 3D (physical) world:

$$ED_{UV} = \sqrt{\sum_{j=1}^S (x_{Uj} - x_{Vj})^2} \quad (1)$$

where x_{Uj} and x_{Vj} are the abundance values of species j in plots U and V , respectively, S is the total number of species recorded in these two plots: $S = |S_U \cup S_V|$, and S_U is the set of species in plot U .

However, community ecologists have repeatedly argued that this coefficient **may provide misleading results for species abundance data containing zeros** (e.g. Orlóci 1972, 1978; Legendre and Gallagher, 2001). As an example, let us consider an artificial community composition matrix composed of four species ($S1$ – $S4$) in three plots (U – W):

	U	V	W
S1	1	0	3
S2	2	0	6
S3	0	1	0
S4	0	2	0

If we use Euclidean distance to measure dissimilarity, we find that the distance between plots U and W , which share species $S1$ and $S2$, is larger than that between plots U and V , which have no species in common: $ED_{UV} = 3.162$; $ED_{UW} = 4.472$; $ED_{VW} = 7.071$. This is counter-intuitive ecologically, because the plots U and W contain the same species while plot V hosts a unique set of species. That is, abundance differences completely override a more fundamental issue: agreement in presence of species. This effect may be more substantial for large data matrices in which many species may easily have just a few records leading to sparse matrices predominantly filled up with zeros (Legendre and Gallagher, 2001).

In order to eliminate the problems inherent to the Euclidean distance, ecologists have developed a rich arsenal of alternative coefficients (see Legendre and Legendre, 2012, for a review). These indices incorporate some operation involving data standardization, i.e. modification of data such that each new score depends on other values in the matrix. If the plot vectors (columns in the example above) are first standardized to unit length by dividing each value with the length of the vector according to

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$x'_{Uj} = x_{Uj} / \sqrt{\sum_{j=1}^S x_{Uj}^2}$, and then the Euclidean distance is calculated from the normalized quantities x'_{Uj} , we get the chord distance (Orlóci, 1967) given by the formula:

$$CH_{UV} = \sqrt{\sum_{j=1}^S \left(\frac{x_{Uj}}{\sqrt{\sum_{j=1}^S x_{Uj}^2}} - \frac{x_{Vj}}{\sqrt{\sum_{j=1}^S x_{Vj}^2}} \right)^2} = \sqrt{\sum_{j=1}^S (x'_{Uj} - x'_{Vj})^2} \quad (2)$$

CH is equivalent to the (Euclidean) length of the chord between two objects (plots) projected onto the surface of a hypersphere of unit radius (Orlóci, 1978; Legendre and Gallagher, 2001). Therefore, in the above example, while the Euclidean distance between U and W is 4.472, their chord distance is zero ($CH_{UW} = 0$), because these plots contain the same species in the same proportions. Since plot V has no species in common with plots U and W , we get the maximum distance between them ($CH_{UV} = CH_{VW} = \sqrt{2} \cong 1.414$). Therefore, for an ecologist this index captures information on community composition in a much more meaningful way than ED .

Another measure of multivariate plot-to-plot dissimilarity that can be calculated by first transforming the plot vectors in an appropriate way and then taking the Euclidean distance of the transformed vectors is the **Hellinger distance** (Legendre and Gallagher, 2001). In this case, the raw values x_{Uj} are first transformed by dividing each value by the plot sum and then taking the square root of the resulting values such that $x''_{Uj} = \sqrt{x_{Uj} / \sum_{j=1}^S x_{Uj}}$. Then, the Euclidean distance is calculated from the transformed quantities x''_{Uj} as:

$$HD_{UV} = \sqrt{\sum_{j=1}^S \left(\sqrt{\frac{x_{Uj}}{\sum_{j=1}^S x_{Uj}}} - \sqrt{\frac{x_{Vj}}{\sum_{j=1}^S x_{Vj}}} \right)^2} = \sqrt{\sum_{j=1}^S (x''_{Uj} - x''_{Vj})^2} \quad (3)$$

Raw data may be transformed by many other ways, however. The formula suggested by Bray and Curtis (1957) implies relativization of species-wise differences by the total abundance of species in the two plots:

$$BC_{UV} = \frac{\sum_{j=1}^S |x_{Uj} - x_{Vj}|}{\sum_{j=1}^S (x_{Uj} + x_{Vj})} \quad (4)$$

This index reflects the proportion of the total species abundances in which the two plots differ. For the above example, BC also outperforms ED because the maximum distance is obtained when the plots being compared have no species in common ($BC_{UV} = 1$ and $BC_{VW} = 1$), whereas $BC_{UW} = 0.5$. This latter example suggests that, unlike CD , BC takes the value zero only if the two plots being compared are identical.

These three coefficients illustrate pretty well that, although dissimilarity may appear an intuitively simple concept, there is no single, unequivocal way for its measurement. The literature of numerical ecology treats many more, even hundreds of dissimilarity functions (see e.g., Orlóci, 1978; Podani, 2000; Legendre and Legendre, 2012) and selection among them is often arbitrary, dictated by fashion, availability in commercial software or personal preference. The choice of a dissimilarity index best suited for a specific ecological problem is a complex question which does not have clear and unambiguous answer. However, while these references provide some information for ecologists to facilitate decision, the properties of even the best known indices are not fully understood.

The aim of this paper is thus to review some of the properties of the Bray-Curtis dissimilarity relevant for ecologists. The paper is

organized as follows: first, we discuss the relationships of the Bray-Curtis dissimilarity with the Canberra dissimilarity family (*sensu* Podani, 2000). Next, we show the ability of the Bray-Curtis dissimilarity to conform to a generalization of Dalton's (1920) principle of transfers to a pair of plots.

2. An unconventional genealogy of the Bray-Curtis dissimilarity

The Euclidean distance is a special case of a more general parametric family of dissimilarity functions called Minkowski distance:

$$MNK_{UV} = \sqrt[\alpha]{\sum_{j=1}^S |x_{Uj} - x_{Vj}|^\alpha} \quad (5)$$

where $\alpha \geq 1$. For $\alpha = 2$, we have the Euclidean distance. For $\alpha = 1$, we obtain the so-called city-block (or Manhattan) distance, which is the sum of absolute differences in species abundances:

$$CB_{UV} = \sum_{j=1}^S |x_{Uj} - x_{Vj}| \quad (6)$$

An advantage of this formula over EU is that species-wise differences are not exaggerated by squaring (Orlóci, 1972). Division by the number of species (or, more generally, characters) produces the average contribution of species to the coefficient, known in multivariate analysis as 'mean character difference' (Cain and Harrison, 1958):

$$MC_{UV} = \frac{1}{S} \sum_{j=1}^S |x_{Uj} - x_{Vj}| \quad (7)$$

The Canberra distance is then derived from the city-block distance by standardizing separately the absolute difference for each species by the sum of the species abundances in both plots (Lance and Williams, 1967):

$$CD_{UV} = \sum_{j=1}^S \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (8)$$

The range of the Canberra distance is $[0, S]$ which may be normalized to $[0, 1]$ by dividing CD with the number of species S . That is, by weighting all single-species dissimilarity components $|x_{Uj} - x_{Vj}| / (x_{Uj} + x_{Vj})$ by $1/S$ we obtain

$$NC_{UV} = \frac{1}{S} \sum_{j=1}^S \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (9)$$

Two additional members of the 'Canberra family', here termed 'modified Canberra 1' and 'modified Canberra 2' respectively, are derived by normalizing the absolute differences $|x_{Uj} - x_{Vj}|$ with the maximum abundances assumed by the species in the two plots, $\max\{x_{Uj}, x_{Vj}\}$:

$$MC1_{UV} = \sum_{j=1}^S \frac{|x_{Uj} - x_{Vj}|}{\max\{x_{Uj}, x_{Vj}\}} \quad (10)$$

and

$$MC2_{UV} = \frac{1}{S} \sum_{j=1}^S \frac{|x_{Uj} - x_{Vj}|}{\max\{x_{Uj}, x_{Vj}\}} \quad (11)$$

The similarity form of Eq. (11), i.e. $1 - MC2$, is generally known as the Pinkham-Pearson coefficient (Podani, 2000).

An additional index similar to Eq. (10) is known as the Marczewski-Steinhaus coefficient (Holgate, 1971; Levandowsky, 1972):

$$MS_{UV} = \frac{\sum_{j=1}^S |x_{Uj} - x_{Vj}|}{\sum_{j=1}^S \max\{x_{Uj}, x_{Vj}\}} \quad (12)$$

However, in this formula there is a **separate summation** for the numerator and the denominator. Note also that the numerator of the Marczewski-Steinhaus coefficient (i.e. the ‘operational’ part of the index *sensu* Legendre, 2014) is identical to that of the Bray-Curtis coefficient. In this framework, a frequent characteristic of many dissimilarity coefficients is that they are formulated in terms of a ratio where the numerator summarizes the amount of plot-to-plot dissimilarity depending on the purpose of the study, while the denominator scales the index to values between 0 and 1 (Legendre, 2014). Thus, the main difference between MS and BC is that they are normalized to the range [0, 1] by distinct scaling factors. Therefore, for species presence and absence data, the Marczewski-Steinhaus coefficient reduces to the Jaccard dissimilarity

$$JAC_{UV} = \frac{b+c}{a+b+c} \quad (13)$$

whereas the Bray-Curtis dissimilarity simplifies to the Sørensen dissimilarity:

$$SOR_{UV} = \frac{b+c}{2a+b+c} \quad (14)$$

where a , b and c denote the matching/mismatching components of a 2×2 contingency table: for two plots U and V , a is the number of species present in both plots, b is the number of species present only in plot U and c is the number of species present only in plot V , such that $a+b+c=S$, i.e. the total number of species in the two plots. Note that the fourth component of the contingency table d , which represents the number of joint absences (i.e. the species absent from both plots being compared but found in other plots of the community composition matrix), is only rarely used in community ecology for the calculation of dissimilarity measures (see Tamás et al., 2001). Therefore, in this paper we will exclude joint absences from the calculation of all presence/absence or abundance-based dissimilarity coefficients.

A desirable property for a dissimilarity index is its ability to be additively decomposed into species-level values, also known as the *sum-property* (Ricotta, 2010). In this way, ecologists can see which species contribute most to plot-to-plot dissimilarity. It is easily shown that Eqs. (6)–(11) conform to the sum property. To show that the Bray-Curtis dissimilarity also conforms to the sum property, we can rewrite this measure as:

$$BC_{UV} = \sum_{j=1}^S \frac{|x_{Uj} - x_{Vj}|}{\sum_{j=1}^S (x_{Uj} + x_{Vj})} = \sum_{j=1}^S w_j \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (15)$$

where $w_j = (x_{Uj} + x_{Vj}) / \sum_{j=1}^S (x_{Uj} + x_{Vj})$ with $0 \leq w_j \leq 1$ and $\sum_{j=1}^S w_j = 1$.

Hence, according to Eq. (15), the Bray-Curtis dissimilarity can be interpreted as a normalized version of the Canberra distance in which the contribution of species j to overall plot-to-plot dissimilarity $|x_{Uj} - x_{Vj}| / (x_{Uj} + x_{Vj})$ is weighted by the pooled abundance of j in plots U and V divided by the total species abundances in U and V . Therefore, unlike Eq. (9) in which all species assume equal importance irrespective of their abundances in U and V (i.e. all weights are equal to $1/S$), in Eq. (15) the contribution of species j to overall dissimilarity is weighted by its relative abundance in the pooled pair of plots.

To illustrate this point with an example, take two plots (U and V) with four species ($S1$ – $S4$):

	U	V
S1	4	2
S2	1	1
S3	5	3
S4	10	6

Here, the weight for the fourth species, $w_{S4} = 16/32$, is much higher than that for the third species, $w_{S3} = 8/32$, even though the term $|x_{Uj} - x_{Vj}| / (x_{Uj} + x_{Vj})$ is the same for both species.

Similarly to the Minkowski distance, which is a generalization of both the Euclidean distance and the city-block distance, we can define a new dissimilarity coefficient termed ‘generalized Canberra dissimilarity’ which includes the weighted mean in Eq. (15) and the unweighted mean in Eq. (9) as special cases of the following formula:

$$GC_{UV} = \sum_{j=1}^S \pi_j \frac{|x_{Uj} - x_{Vj}|}{(x_{Uj} + x_{Vj})} \quad (16)$$

with $0 \leq \pi_j \leq 1$ and $\sum_{j=1}^S \pi_j = 1$. The values of the species-specific weights π_j may embody different ecological variables related to the species conservation value, its phylogenetic and/or functional originality, or to any other biological parameter that is thought to influence ecosystem functioning at the plot scale. For $\pi_j = 1/S$, GC is identical to the normalized Canberra coefficient, while for $\pi_j = (x_{Uj} + x_{Vj}) / \sum_{j=1}^S (x_{Uj} + x_{Vj})$, GC reduces to the Bray-Curtis dissimilarity. Likewise, for species presence and absence scores, if all weights π_j are set equal to $1/S$, GC simplifies to the Jaccard dissimilarity, while for $\pi_j = w_j$, GC reduces to the Sørensen dissimilarity (proof in Appendix 1 in the Supplementary material).

In the same way, we can define a generalized version of the Marczewski-Steinhaus coefficient:

$$GMS_{UV} = \sum_{j=1}^S p_j \frac{|x_{Uj} - x_{Vj}|}{\max\{x_{Uj}, x_{Vj}\}} \quad (17)$$

with $0 \leq p_j \leq 1$ and $\sum_{j=1}^S p_j = 1$ for which, setting $p_j = 1/S$, Eq. (17) reduces to the MC2 coefficient, while for $p_j = (x_{Uj} + x_{Vj}) / \sum_{j=1}^S \max\{x_{Uj}, x_{Vj}\}$ the classical MS coefficient is obtained.

3. A modified principle of transfers for a pair of plots

In the previous section we showed that the Bray-Curtis dissimilarity is sensitive to differences in abundance between species, and that abundant species are weighted more than rare species. The aim of this section is now to analyze how BC is influenced by differences in species abundances between plots.

The question whether a given index is a suitable measure of dissimilarity is usually answered axiomatically by assessing whether the index meets some properties that are intuitively considered to be desirable for a dissimilarity measure. Here, our aim is to characterize the behavior of dissimilarity measures with a focus on a modified version of Dalton’s (1920) principle of transfers.

In its very essence, given a species j with (absolute) abundances x_{Uj} and x_{Vj} in plots U and V , respectively, such that $x_{Uj} \geq x_{Vj}$, all else being equal, dissimilarity is decreased if the quantity δ is transferred from x_{Uj} to x_{Vj} so long as that transfer does not reverse the ranking of the two abundances $x_{Uj} - \delta \geq x_{Vj} + \delta$ (which is tantamount saying that $\delta \leq (x_{Uj} - x_{Vj})/2$). Consistently with our intuitive notion of dissimilarity, this transfer property states that, for a given pair of plots, dissimilarity is *decreased* when abundance is transferred from a species in one plot to the same species in another plot in which that species is less abundant.

We empirically tested whether the indices *EU*, *CH*, *HD*, *CB*, *CD*, *NC*, *MC1*, *BC* and *MS* conform to this principle using the following procedure: let U and V be a pair of plots, both composed of five species with abundances $U = (10, 20, 30, 40, 50)$ and

$V = (0, 0, 0, 0, 0)$, respectively, such that the total abundance in the two plots is $\sum_{j=1}^S x_{Uj} + \sum_{j=1}^S x_{Vj} = 150$.

First, the species abundances in U are transferred step by step to plot V . At each step, five units of abundance are randomly transferred from U to the corresponding species in V until both plots reach the same abundance distribution: (5, 10, 15, 20, 25). After each transfer, the dissimilarity between plots U and V is calculated and the result is plotted against the proportion of species abundances in plot V , $p(V) = \sum_{j=1}^S x_{Vj}/150$. Note that, to make the calculations easier, at the beginning of the transfer procedure, plot V is completely empty. However, this choice does not reduce the generality of our analysis.

The results of this operation are shown in Fig. 1. For each dissimilarity coefficient, the same random sequence of transfers was used (see Appendix 2 in the Supplementary material). Since for several of the dissimilarity coefficients the resulting curve is specific to the random realization used, the behavior of the coefficients becomes more obvious by examining a second non-random sequence of transfers as well. In this, the five units are always transferred from the smallest value in U to the corresponding species in V : first $10 \rightarrow 5$, next $20 \rightarrow 15$ and $15 \rightarrow 10$, etc. (see Appendix 2 in the Supplementary material).

Apart from the chord and the Hellinger distances, all other dissimilarity coefficients decrease more or less regularly when species abundances are transferred from plot U to plot V . For EU , CD and HD , the non-random sequence of transfers provides an upper bound with respect to the corresponding random sequence, whereas for CD , NC and $MC1$ both profiles are ordered in the opposite way. This difference emphasizes once more the different behavior of the Canberra dissimilarity family compared to the Euclidean-like measures, such as CD or HD .

For CB , BC and MS the resulting profiles are independent on the way abundances are transferred from plot U to plot V . However, the city-block distance and the Bray-Curtis dissimilarity are the sole

coefficients with linear response to the transfer of abundances (proof in Appendix 1 in the Supplementary material). The main difference between these two coefficients is that CB has no upper limit, while BC measures dissimilarity in the range $[0, 1]$. Note also that in Fig. 1 the coefficients CB and NC show an identical behavior, as dividing the values of the Canberra distance by a constant (i.e. species richness S) does not change the pattern of the index values vs. $p(V)$.

4. Discussion

Ecologists have proposed an extensive arsenal of coefficients for summarizing different aspects of plot-to-plot dissimilarity. In this view, the behavior of such measures must be understood to assess whether these measures allow useful biological distinctions between a pair of plots. In this paper we thus reviewed some of the properties of the Bray-Curtis dissimilarity that may be relevant in the context of ecology.

We started from the suggestion that the BC index is additively decomposable into species-level contributions (see also Clarke, 1993; Podani, 1998). The formalism used for demonstrating the species-level decomposition of the BC index allowed us to define a new family of dissimilarity coefficients termed 'generalized Canberra dissimilarity' which includes the normalized Canberra and the Bray-Curtis dissimilarities as special cases.

Generalized dissimilarity coefficients have a long tradition in ecology and multivariate analysis. Apart from the Minkowski distance, Grassle and Smith (1976) introduced a family of probabilistic overlap indices, which is based on the notion of expected species shared (ESS). Given two plots U and V , ESS is defined as:

$$ESS_{UV|m} = \sum_{j=1}^S \left(1 - (1 - p_{Uj})^m\right) \left(1 - (1 - p_{Vj})^m\right) \quad (18)$$

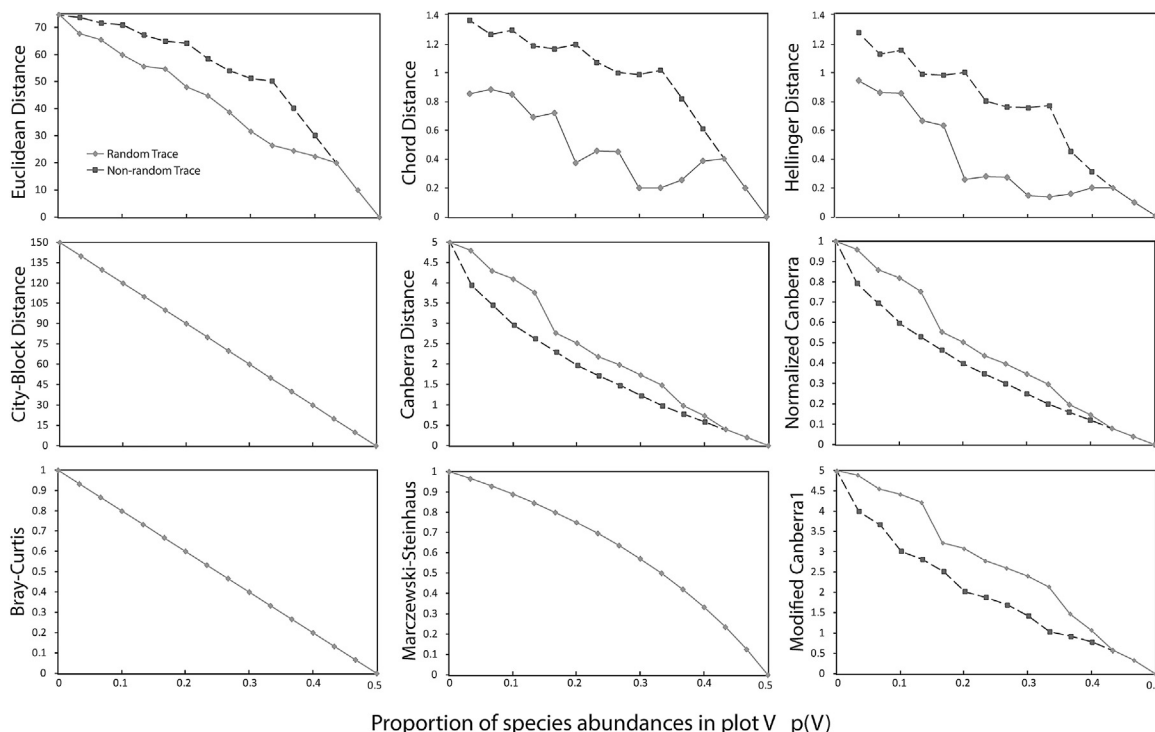


Fig. 1. Graphical illustration of the agreement of the dissimilarity indices EU , CH , HD , CB , CD , NC , BC , $MC1$ and MS to the modified principle of transfers. Note that the Chord and the Hellinger distances are not defined for the empty plot $V = (0, 0, 0, 0, 0)$. In all cases in which the random sequence of transfers (continuous line) and the non-random sequence of transfers (dotted line) produce an identical trace, the trace of the non-random sequence is omitted.

where p_{Uj} is the relative abundance of species j in plot U : $p_{Uj} = x_{Uj} / \sum_{j=1}^S x_{Uj}$. ESS represents the expected number of species shared by plots U and V , if m individuals are selected randomly with replacement from both plots. To get a statistically valid index of similarity in the range $[0, 1]$ ESS needs to be normalized as:

$$NESS_{UV|m} = \frac{ESS_{UV|m}}{(ESS_{UU|m} + ESS_{VV|m})/2} \quad (19)$$

while its complement $1-NESS$ represents a normalized probabilistic dissimilarity measure (Trueblood et al., 1994; Ricotta and Bacaro, 2010).

The parametric formulation of $NESS$ allows for different weights to be attributed to species differing in abundance. The main difference between the parameter m in Eq. (18) and the weights π_j in Eq. (16) is that the former has a probabilistic interpretation, whereas the species-specific weights of the generalized Canberra dissimilarity are more flexible as they may reflect a much larger array of ecological drivers.

Using profile diagrams, we also showed the ability of the Bray-Curtis dissimilarity to conform to a modified version of Dalton's (1920) principle of transfers. While in ecological theory, Dalton's principle of transfers is generally used to investigate how diversity or evenness changes if abundance is transferred from an abundant species to a less abundant species within the same plot (see e.g. Patil and Taillie, 1982), in our work the principle of transfers is used to summarize how dissimilarity changes if abundance is transferred from a plot with high total abundance of species to a less abundant plot.

Unlike most dissimilarity measures, the Bray-Curtis and the city-block coefficients show linear response to the transfer of abundance from a given species in one plot to the same species in another plot in which the species is less abundant. Five other coefficients (EU , CD , NC , $MC1$ and MS) show a rather gradual, although nonlinear change along with the transfer of abundances. This is an indication of the inconsistent behavior of these formulae within the range of abundance differences. Four of these indices change in an irregular fashion. That is, the observed decrease in dissimilarity is not proportional to changes in abundance. Obviously, such an irregularity is undesirable ecologically.

MS is the only coefficient for which the dissimilarity profile is a concave function of abundance transfer (see Appendix 1 in the Supplementary material), meaning that the first steps of the sequence of transfers caused smaller changes than the last steps. In other words, transfer of abundances between two plots with similar abundance structure affects plot-to-plot dissimilarity more than the same transfer of abundances from a plot with high total abundance of species to another plot with much less abundant species. Whether this behavior is biologically reasonable is left to the judgment of the practitioner.

The worst case in the group of measures examined is represented by the chord and the Hellinger distances, which exhibit extremely irregular profiles. This is due to the fact that in both cases dissimilarity is calculated after non-linear transformation of species abundance data. Therefore, CD and HD are not appropriate for summarizing plot-to-plot dissimilarity whenever a linear relationship between dissimilarity and the proportion of species abundances in both plots is required. The latter observation is in accordance with the findings of Faith et al. (1987) as well.

To conclude, ecologists are faced with a multitude of dissimilarity indices, but unfortunately there is no perfect function capable of summarizing all aspects of biological dissimilarity. By reducing the structure of a multidimensional set such as a biological community into a single number, information is

necessarily lost. Therefore, the selection of an adequate dissimilarity index largely depends on the available data and on the objective of the study. Accurate evaluation of dissimilarity measures in terms of their basic properties is thus a necessary condition to ensure that they really measure what we want to measure (Sherwin et al., 2006). Then, as stressed by Pavoine (2016), "it would be easier to accept that a variety of indices is needed to answer a variety of ecological questions".

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Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecocom.2017.07.003>.

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