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A link between ecological diversity indices and measures of biodiversity

János Izsák a,*, László Papp b

Abstract

The practice of environmental planning and protection frequently necessitates the quantification of ecological diversity. Traditional 'ecological diversity indices' are based on the abundances of species present. However, such indices are insensitive to taxonomic or similar differences. With equal species abundances they measure the species richness (species number) only. Conversely, so-called 'biodiversity indices' are based on species differences, but are insensitive to the abundance conditions. The quadratic entropy index is the only ecological diversity index, the value of which reflects both the differences 'and' abundances of the species. When a species list is given without abundance data, then, using the quadratic entropy index and postulating equal abundances, one gets the only biodiversity index derived from a traditional ecological index of diversity. Its extensive form is identical with the sum of differences or distances between the species present. This index trivially satisfies set monotonicity, an important property for biodiversity indices. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Biodiversity is a central idea in the practice of quantifying the ecological status of different biotops by known abundances of species. However, in large-scale environmental protection, the species abundances are mostly unknown. In such cases we have to use so-called biological diversity measures, which are based on taxonomic relations or similar differences of species only. Here abun-

E-mail address: ijanos@fs2.bdtf.hu (J. Izsák).

dance conditions of the species are unessential. As for the term 'biological diversity', it dates back to the early 1980s. Perhaps Lovejoy (1980) used it first in the sense of the number of species present. The contracted form 'biodiversity' was coined by Rosen in 1985 (cf. Harper and Hawksworth, 1995). As these authors write, for practical purposes 'biodiversity' can be considered synonymous with Lovejoy's 'biological diversity'. (The history of both expressions is summarized in an excellent book edited by Hawksworth, 1995). In the recent past, biodiversity measures other than that based on the number of species present (species richness) have been introduced. We should

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^a Berzsenyi Dániel College, Department of Zoology, Károlyi G. tér 4, H-9701, Szombathely, Hungary

b Hungarian Natural History Museum, Department of Zoology, Baross u. 13, H-1088, Budapest, Hungary

^{*} Corresponding author. Tel.: +36-94-313892; fax: +36-94-312248.

like to emphasize that each of these measures implicates a somewhat different definition of biodiversity. For example, Weitzman (1992) proposed a measure, which takes account of the species set and distances between species, but ignores species abundances. Species distances are used to define distances between a simple species and a set of species. On a similar basis, Solow et al. (1993) introduced a 'preservation measure', pertaining to the set of species to be preserved. Although not a diversity measure, it correlates with the expected diversity loss by eliminating a subset of species. As both of these newer measures disregard species abundances, they are close in spirit to the index proposed below. Krajewski (1994), who compared some index properties on crane species data, provides a review of biodiversity measures.

All these biodiversity indices are based on new conceptions of species diversity and are not linked to traditional diversity indices. Another means of amplifying the concept of diversity is to consider the diversity of functional connections between species. For example, Jizhong and Shijun (1991) elaborated a new diversity index based on species abundance and functional relations between species. The new ecosystem diversity is defined as the sum of species diversity and structural diversity. Naturally, for concrete applications one should be informed about figures on numerous relations.

Turning to traditional indices of species diversity, we recall that the diversity of birds, moths, vascular plants and other, relatively homogeneous taxa depends intuitively both on the number of occurring species and the evenness of the distribution of individuals among the species. Numerous measures of ecological diversity (or community diversity, species diversity) have been introduced in the decades past (for a review see Grassle et al., 1979 and Magurran, 1988). The most popular diversity index is perhaps the Shannon–Wiener index with the formula

$$-\sum_{i=1}^{s} p_i \log p_i$$

1where s stands for the number of species and p_i (i = 1,..., s) denotes the (theoretical) probability of an individual belonging to the ith species.

Other widely used diversity indices include the reciprocal Simpson index and the Gini-Simpson index. Introducing the quantity

$$D := \sum_{i=1}^{s} p_i^2$$

2these indices can be formulated as 1/D and 1-D, respectively. Note that the traditional diversity indices do not depend on taxonomic relations between species.

2. A gap between diversity indices and biodiversity measures

Diversity indices will continue to play an important role in the future. However, a gap remains between the indices of the old concept and the indices connected with the newer notions of 'biological diversity' or 'biodiversity'. Namely, ecological diversity indices are scarcely mentioned in the literature of biodiversity, notwithstanding the fact that one can take the species richness (number of species) for a species diversity index. To make a link between these diversity concepts, let us mention some specific properties of the ecological diversity indices. Fixing the number of species, one arrives at the evenness component of species diversity. Numerous measures of evenness are in use in ecology and in other disciplines (Pielou, 1975; Magurran, 1988; Egghe and Rousseau, 1991). By definition, so-called 'heterogeneity indices' reflect both the evenness and richness components of diversity. (It would be more accurate to speak of evenness and richness 'dimensions', because the heterogeneity indices are not simple functions of richness and evenness measures.) Some authors take only the heterogeneity indices for genuine diversity indices.

The value of a traditional heterogeneity index L with equal probabilities in the argument can be considered a richness measure. This is because these indices are monotone increasing functions of the number of species s:

$$L(1/s, 1/s,..., 1/s)$$

 $\leq L(1/(s+1), 1/(s+1),..., 1/(s+1))$

With regard to 'biological diversity' in its current senses, the abundance conditions and the evenness component are irrelevant with these. This one-sidedness is explainable by three conditions. First, in many cases the correct data on abundances are unknown. Often the only valuable data is the number of species, or its estimate. Second, focusing on the maintenance and conservation problems, the abundances (within certain limits) are irrelevant. Third, the comparison of abundances is largely meaningless between systematically remote organisms (ants and elephants). In these circumstances, we can attribute the same abundance value to all occurring species.

Or, in what amounts to the same thing, we register only the presence of the species. As noted above, by these conditions the traditional heterogeneity indices can be considered as single richness indices, since they are monotone increasing functions of the number of species. That is, comparing the biodiversity of different study areas, the diversity values 'will rank the communities according to the s number of the occurring species'; if the abundances are equal, then the application of the traditional diversity indices gives no more information than the number of species alone does. On the other hand, the sophisticated biodiversity measures emerging in the recent past take into account the differences between the species and neglect the abundance conditions. Some of these measures relate to taxonomic trees containing the species present. For instance, Vane-Wright et al. (1991) defined the 'distinctiveness'; and Faith (1992) introduced the 'phylogenetic diversity' of a taxonomic tree. The former is based on taxonomic distances, the latter on 'feature mismatches' (for further details see Faith, 1995). One can conclude that there is a gap between traditional diversity indices and biodiversity measures.

Studying these biodiversity measures, one concludes that none of them are based on the previously mentioned ecological diversity indices introduced long ago and used intensively also today. The explanation follows from the above mentioned properties of the traditional diversity indices. With a fixed number of species, the tradi-

tional diversity indices are sensitive to species abundances and insensitive to species differences. Conversely, biodiversity measures are sensitive to the latter and neglect the abundance conditions.

3. A possible link between diversity indices and biodiversity measures

We propose here a possible link between the realm of diversity indices and measures of biodiversity. We have previously reported on the ecological application of the quadratic entropy diversity index Q (Izsák and Papp, 1995). Let d_{ij} (i, j = 1,..., s) be the 'differences' between species (not necessarily fulfilling the distance axioms), with $d_{ij} = d_{ji}$, and $d_{ii} = 0$. The quadratic diversity index (Rao, 1982) is defined as the quadratic form

$$Q := \sum_{i=1}^{s} \sum_{j=1}^{s} d_{ij} p_{i} p_{j} = p' \Delta p$$

Q expresses the expectancy of the difference between two, randomly chosen individuals. In the rather special case, where $d_{ij} = 1$ for all $i \neq j$ and $d_{ii} = 0$, it is easy to see that Q is equal to the Gini-Simpson index 1 - D.

A simple way to generate species differences can be based on the following definition of the d_{ij} taxonomic distance of two species: let d_{ij} stand for the number of internodes from the species level to the lowest level of the taxonomic tree where a common ancestor of species i and j exists. For example, in Fig. 1 the distance between a_1 and a_4 is 3.

Another example can be the introduction of tentative differences (not necessarily distances) between species based on some property. For example, relating to a drosophilid assemblage, types take the following of resources: saprophagous (s), mycophagous (m), frugivorous (f), commensalist (c), sap feeder (sf), herbivorous (h) and of unknown habits (u). A tentative difference matrix is schemed in Fig. 2. Note, that we are speaking here of differences only, and not of distances. Indeed, the distance axioms are in this case not fulfilled. For example, $d_{\rm sf,u} = 5 > d_{\rm sf,s} +$ $d_{\rm su} = 4$.

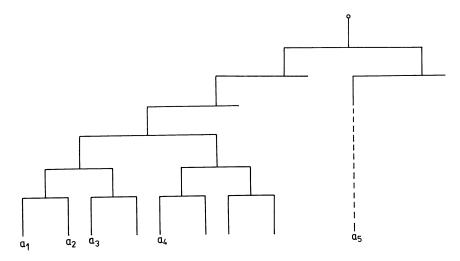


Fig. 1. A taxonomic tree with fix levels. For taxonomic distances of species $a_1, ..., a_5$ see the text.

When the same hypothetical or formal abundance values are attributed to each abundance, then, the quadratic entropy index will be a function of the number of species and their taxonomic relations. In this special case Q can be written in the form

$$J: \frac{1}{s^2} \sum_{i, j} d_{i, j}$$

expressing the mean taxonomic distance between two randomly chosen 'species'. (We enumerate here all pairs two-fold; this is a technical question.) It is an important condition, that 'the relations between species influence *J*, as opposed to other ecological diversity indices'. Thus, *J* links ecological diversity indices and biodiversity measures.

Concerning index properties, set monotonicity is a property generally required for biodiversity measures. Denoting a measure by I, this property means that $I(A \cup \{x\}) > I(A)$. This ensures that the index value will increase by adding a new species to a species set A. The index J does not satisfy this requirement. For example, taking the set $A := \{a_1, a_3, a_4\}$ and species a_2 in Fig. 1, $J(A \cup \{a_2\}) = (1/24) \cdot 2(d_{1,2} + d_{1,3} + d_{1,4} + d_{2,3} + d_{2,4} + d_{3,4}) = (1/8) \cdot (1 + 2 + 3 + 2 + 3 + 3) = 14/8 < J(A) = (1/2^3) \cdot 2(2 + 3 + 3) = 2$. That is, the mean difference J is not an ideal biodiversity index. To

change from this intensive measure to its extensive counterpart, we introduce the measure

$$F:=s^2\cdot J=\sum_{i,j}d_{ij}$$

which is the sum of the differences of species. The set monotonicity applies to F, being that for any set A and element x

$$F(A \cup \{x\}) = \sum_{i,j} d_{ij} + \sum_{i} d_{i,s+1} > \sum_{i,j} d_{ij} = F(A)(x \notin A)$$

where $d_{i,s+1}$ (i = 1,..., s) stands for the difference of the elements in A and $a_{s+1} := x$.

We can conclude that the sum of the species differences is a more suitable measure of biodiversity than the mean of differences.

	.	m	f	c	sf	h	и
s	0	1	1	1	2	1	2
m		0	2	2	3	2	3
f			0	2	1	2	3
c				0	3	2	3
sf					0	3	5
h						0	3
u							0

Fig. 2. Difference matrix for the different resource types. For abbreviations see the text.

Remarkably, neither J nor F is a richness index insofar as they are 'not' monotone increasing functions of the number of species. Instead, favorably, their values are determined simultaneously by the species number and the differences between the species. This contrasts with the properties of diversity indices with equal species abundances (see Section 2). The above counter-example on set monotonicity for J is also applicable in the present case. A counter-example for F: take $C = \{a_1, a_2, a_3\}$ and $D = \{a_1, a_5\}$ in Fig. 1. Then, F(C) = 10 < F(D) = 12, notwithstanding that C contains more species than D.

4. Conclusion

Numerous measures of biodiversity are in use, satisfying different advantageous statistical properties. However, a gap remains between these measures and the traditional diversity indices. The former are insensitive to abundance conditions, the latter do not take into account the distances or differences between species or other taxa. The only exception is the quadratic entropy index Q, which is a function both of abundances and taxonomic distances or differences. Taking equal abundance values for the species, one arrives at the mean distance of species in the set in question, J. The assumption of random choice of a species or a set of species, regardless of abundance conditions, that is taking equal abundances is in some cases reasonable. For example, a specific toxic substance may 'choose' a species regardless of the latter's abundance. Index J bridges the gap between ecological diversity indices and biodiversity measures in the modern senses. However, J does not satisfy the property of set monotonicity, which is essential for biodiversity measures. The extensive version F is also a link between the two types of diversity measures. Moreover, it satisfies the requirement of set monotonicity. Thus, F is the more appropriate biodiversity measure.

As demonstrated above, the d_{ij} differences are not necessarily taxonomic distances, or distances in general, satisfying the distance axioms. They may represent differences in life style, diet or

other properties. Thus, establishing different d_{ij} values, one can obtain a variety of biodiversity measures. Applying the measure F and similar measures in concrete field studies, it will be possible to gain insight into their usefulness in biodiversity research.

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References

Egghe, L., Rousseau, R., 1991. Transfer principles and a classification of concentration measures. J. Am. Soc. Inf. Sci. 42, 479–489.

Faith, D.P., 1992. Conservation evaluation and phylogenetic diversity. Biol. Conserv. 61, 1–10.

Faith, D.P., 1995. Phylogenetic pattern and the quantification of organismal biodiversity. In: Hawksworth, D.L. (Ed.), Biodiversity, Measurement and Estimation. Chapman and Hall, London, pp. 45–58.

Grassle, J.F., Patil, G.P., Smith, W., Taillie, Ch., 1979. Ecological Diversity in Theory and Practice. International Co-operative House, Fairland, MD.

Harper, J.L., Hawksworth, D.L., 1995. Preface. In: Hawksworth, D.L. (Ed.), Biodiversity, Measurement and Estimation. Chapman and Hall, London, pp. 5–12.

Hawksworth, D.L. (Ed.), 1995. Biodiversity, Measurement and Estimation. Chapman and Hall, London.

Izsák, J., Papp, L., 1995. Application of the quadratic entropy indices for diversity studies of drosophilid assemblages. Environ. Ecol. Stat. 2, 213-224.

Jizhong, Z., Shijun, M., 1991. An index of ecosystem diversity. Ecol. Mod. 59, 151–163.

Krajewski, C., 1994. Phylogenetic measures of biodiversity: a comparison and critique. Biol. Conserv. 69, 33–39.

Lovejoy, T.E., 1980. Changes in biological diversity. In: Barney, G.O. (Ed.), The Global 2000 Report to the President, Vol. 2 (The Technical Report). Penguin Books, Harmondsworth, pp. 327–332.

Magurran, A.E., 1988. Ecological Diversity and Its Measurement. Croom Helm, London.

Pielou, E.C., 1975. Ecological Diversity. Chap. 1. Wiley, New York.

Rao, C.R., 1982. Diversity and dissimilarity coefficients: a unified approach. Theor. Pop. Biol. 21, 24–43. Solow, A., Polasky, S., Broadus, J., 1993. On the measurement of biological diversity. J. Env. Econ. Manag. 24, 60–68.

Vane-Wright, R.I., Humphries, C.J., Williams, P.M., 1991.

What to protect: systematics and the agony of choice. Biol. Conserv. 55, 235–254.

Weitzman, M.L., 1992. On diversity. Q. J. Econ. 107, 363-