

# THROUGH THE JUNGLE OF BIOLOGICAL DIVERSITY

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## ABSTRACT

Biological diversity would apparently seem the most intuitive and easily studied of all the ecological concepts. However, in practice biodiversity has suffered from great number of definitions that vary with the specific needs of the different researchers, thus making it extremely confusing as an ecological concept. In this paper, I shortly review the concept of biodiversity showing that there exists a substantial ambiguity among ecologists as far as biodiversity conceptualization and evaluation is concerned. I conclude that, due to this major disagreement on its very nature, biodiversity may be defined simply as a set of multivariate summary statistics for quantifying different characteristics of community structure.

**Key Words:** functional diversity, Schur concavity, taxonomic diversity, weak diversity measures

## 1. INTRODUCTION

The relation between biological diversity and ecosystem functions such as productivity, nutrient cycling and storage, carbon sequestration, and stability to perturbations have been studied extensively for many decades and still are the subject of debate (Tilman and Downing, 1994; Grime, 1997; Hooper and Vitousek, 1997; Tilman *et al.*, 1997). This scarcity of univocal results has led to the well-known comments by Hurlbert (1971) on the 'non-concept of species diversity', and by Poole (1974) that diversity measures are 'answers to which questions have not yet been found'.

The main reason for this confusion is that although biodiversity would apparently seem the most intuitive and easily studied of ecological concepts, no proper, generally agreed-on definition and measurement techniques have been formulated. For instance, ecological data are generally multivariate of high dimension, so there is a need for summarization. However, mapping a large data set such as a biological community to a scalar generally results in some loss of information. Therefore, some would argue that diversity indices conceal more than they reveal (Rousseau *et al.*, 1999).

In addition, most researchers believe that diversity as an ecological concept is quite different from diversity as a statistical index. In her review of the book by Grassle *et al.* (1979), 'Ecological Diversity in Theory and Practice', Pielou (1980) wrote: "I was distressed to find that so many people treat 'diversity' and 'diversity index' as synonyms. It will be evidently new to many statisticians that an ecologist studying diversity is not merely engaged in devising, and estimating, an index that is the qualitative

analogue to variance. Ecological diversity is a biological phenomenon. . .". Likewise, in his comment on Patil and Taillie's (1982) paper 'Diversity as a Concept and its Measurement', Sugihara (1982) noted: "To the ecologist, diversity is interesting as a property of state in so far as it has the potential to reflect the nature of the underlying processes and organization that structure the community. Therefore, beyond arbitrary or weakly motivated definitions the scientific interest in and importance of ecological diversity hinges directly on its possible connection with the functioning and organization of communities. . .".

To the contrary, I agree with Molinari (1989) that "Diversity as an unequivocal and inherent property of a biological system does not exist. Instead, as it is the case with any other statistic, diversity values are merely numbers and their relevance to ecological problems must be judged on the basis of observed correlations with other environmental variables". In this paper, I will present a short, non-exhaustive review of the concept of biological diversity reflecting my personal bias that, as an ecological concept, biological diversity has suffered from too great a number and diversity of definitions thus making it very ambiguous. It follows that, from an operational viewpoint, biodiversity may be defined simply as a set of multivariate summary statistics for quantifying different aspects of community structure.

## 2. TRADITIONAL DIVERSITY MEASURES

The first and obvious way for summarizing diversity simply consists in counting the number of species present at a given location. However, it has rapidly become clear that simple estimation of species richness is a very crude estimation of community structure. As an alternative, the distribution of species relative abundances defines biodiversity in a more complete way (Hengeveld, 1996; Ricotta, 2000). Characterizations of these distributions are called diversity measures, of which a great number have been formulated (e.g., Magurran, 1988; Tóthmérész, 1995).

Imagine a plant community or sample composed of  $N$  species, where  $p_i$  is the proportional abundance (measured as number of individuals, dry weight or productivity) of the  $i$ -th species ( $i = 1, 2, \dots, N$ ) such that  $0 \leq p_i \leq 1$  and  $\sum_{i=1}^N p_i = 1$ . Traditional diversity measures are generally computed from the relative abundance vector  $p = (p_1, p_2, \dots, p_N)$  to the exclusion of other differences among species. From a statistical viewpoint, the diversity of a given community is the measure of uncertainty in predicting the relative abundance of species. The ecological rationale behind such measures is that they combine in a non-standard way two components: species richness and evenness. Although each index weighs rare and abundant species differently, high species richness and evenness are both equated with high diversity (Ricotta, 2003).

In this view, in contrast to the piecemeal, invent-an-index approach so rightfully derided by Hurlbert (1971), Patil and Taillie (1982) defined community  $B$  as intrinsically more diverse than community  $A$  *without reference to indices*, provided  $A$  leads to  $B$  by a finite sequence of forward transfers of species abundances from one species to another strictly less abundant species. Formally, let  $A$  and  $B$  be communities with respective species abundance vectors  $p(A)$  and  $p(B)$ . We say that  $A$  leads to  $B$  by a forward transfer of abundances, if there are positive integers  $i$  and  $j$  such that  $p_i(A) > p_j(A) \geq 0$

and

$$p_k(B) = \begin{cases} p_k(A) & \text{if } k \neq i, j \\ p_i(A) - h & \text{if } k = i \\ p_j(A) + h & \text{if } k = j \end{cases} \quad (1)$$

where  $0 \leq h \leq p_i(A) - p_j(A)$ . Such a transfer increases species richness when  $p_j(A) = 0$ , and increases evenness when  $p_j(A) > 0$ . Diversity measures  $\delta$  that satisfy this property are termed ‘Schur-concave’. Given a Schur-concave diversity index,  $\delta(A) \leq \delta(B)$  whenever community  $A$  leads to community  $B$  by a forward transfer of species relative abundances from one species to another strictly less abundant species. This requirement that transferring abundances should increase the index is known in econometrics as Dalton’s ‘principle of transfers’ and was originally proposed in connection with the measurement of income inequality. Here it is worth noting that the most widely used diversity indices, such as the Shannon entropy  $H = -\sum_{i=1}^N p_i \log p_i$  or the Simpson diversity  $1/D$  (where  $D$  is Simpson’s dominance index  $\sum_{i=1}^N p_i^2$ ) are both Schur-concave.

Interestingly, the Shannon index and the Simpson index were developed within the context of communication theory (Shannon, 1948) and cryptanalysis (see Good, 1979, 1982), while their important role in ecological work was recognized some years later by McArthur (1955) and Simpson (1949), respectively. Since then, they have rapidly become the most popular measures of community structure. Also, due to their effectiveness in quantifying the uncertainty of probability distributions far beyond the restricted field of ecology, both measures have been extensively used in areas as different as econometrics, chemometrics, or bibliometrics (Patil and Taillie, 1982; Izsák, 1992).

### 3. TAXONOMIC DIVERSITY

In the early nineties, an intense wave of criticism regarding the concept of diversity as a summary statistic that is obtained from the species relative abundances appeared in the field of conservation biology. For instance, for large-scale environmental protection purposes, data on species abundances are generally unknown. Often the only available data is the number of species. In addition, if our main task consists in targeting places for conservation action (see for example Sarkar and Margules, 2002 and references therein), the information on species abundances is mostly irrelevant and the common treatment of species abundances is largely meaningless in case of systematically remote organisms, such as oaks and orchids (Izsák and Papp, 2000).

Vane-Wright *et al.* (1991) were the first to suggest that, for conservation purposes, we should quantify the phylogenetic relationships amongst species ignoring their relative abundances. Therefore, Vane-Wright *et al.* (1991) proposed a measure of species ‘taxonomic distinctiveness’ that is based on the topology of cladistic classifications. Successively, various refinements of this basic idea have been actively pursued (e.g., Faith, 1992, 1995).

Unfortunately, detailed, fully resolved cladograms are not available for most groups of organisms, and the basic information on species relatedness is often just the set of pairwise taxonomic distances between species. These distances (not necessarily fulfilling the triangle inequality) can be based on morphological differences (Izsák and Papp,

1995), on Linnaean taxonomy (Izsák and Papp, 1995; Warwick and Clarke, 1995), or on more refined molecular biological methods (Crozier, 1992).

Let  $\Delta$  be a species distance matrix, the elements  $d_{ij}$  of which embody the taxonomic distances between the  $i$ -th and the  $j$ -th species, such that  $d_{ii} = 0$  and  $d_{ij} = d_{ji}$  for any  $i \neq j$ . Solow and Polasky (1994) suggested to equate the taxonomic diversity of a given community or species sample to an increasing function of the elements  $d_{ij}$  of  $\Delta$ . Also, they set out three natural requirements that such taxonomic diversity measures should satisfy: first, diversity should not be decreased by the addition of a new species to a given species set  $A$ . Formally, if  $B \subset A$ , then  $\delta(B) \leq \delta(A)$ . This property is called ‘set monotonicity’ (Izsák and Papp, 2000). Next, diversity should not be increased by the addition of a species that is identical to a species already in the set. Finally, diversity should not be decreased by an unambiguous increase in the distances between species. That is, for a one-to-one mapping of  $B$  onto  $A$  such that  $d_{ij}(B) \leq d_{ij}(A)$ , with at least one strict inequality,  $\delta(B) \leq \delta(A)$ . This property is called ‘monotonicity in distance’ (Solow and Polasky, 1994). Based on the above requirements, a straightforward way to collapse the structure of the species distance matrix  $\Delta$  into a summary statistics ( $\Sigma_{\Delta}$ ) is to sum the elements  $d_{ij}$  in  $\Delta$  (Izsák and Papp, 2000):

$$\Sigma_{\Delta} = \sum_{i,j \in \Delta} d_{ij} \quad (2)$$

Additional taxonomic diversity measures that conform to the above requirements were proposed by Weitzman (1992) and Solow and Polasky (1994). Notice that, as discussed in Ricotta (2002a), the only diversity index used to date in the ecological practice that is both set monotone *and* Schur-concave is species richness.

#### 4. FUNCTIONAL DIVERSITY

Another wave of criticism regarding traditional diversity measures is related to the observation that there is no magic direct effect of the number of species *per se* on ecosystem processes; any effect arises from functional differences between species (Diaz and Cabido, 2001). It has been suggested that ecosystems with a greater diversity of functional traits will operate more efficiently in terms of productivity (Tilman, 1999), resilience (Nystrom and Folke, 2001), and resistance to invaders (Prieur-Richard and Lavorel, 2000; Dukes, 2001). Therefore, it might be reasonable to substitute traditional diversity indices with measures of functional diversity that summarize the extent of functional differences in a species pool (Hooper, 1998; Fonseca and Ganade, 2001; Naeem and Wright, 2003).

A common measure of functional diversity is the number of functional groups represented by the species in a community. To cluster species into functional groups, first, a set of characters thought to be of significance for ecosystem functioning is measured for each species obtaining a trait matrix. Next, the trait matrix is converted into a distance matrix. Finally, the distance matrix is clustered with standard multivariate methods to divide species among functional groups (Gitay and Noble, 1997).

Of the problems associated with assigning species to groups perhaps the least tractable are that: (i) the result can depend on the number and type of functional characters that are measured, and this is basically a subjective decision which depends partly on the objective of the study (Diaz and Cabido, 1997; Pillar, 1999; Fonseca and Ganade, 2001),

and (ii) the conclusions on functional diversity will often depend on the arbitrary scale at which differences between species qualify as functionally significant, or, in other words, on how many groups are used (Petchey and Gaston, 2002). An alternative way for summarizing the extent of species functional differences consists in quantifying diversity directly from the functional distance matrix. Based on this suggestion, functional diversity can be computed in a manner similar to the methods by which taxonomic diversity is quantified (Walker *et al.*, 1999; Petchey and Gaston, 2002). However, regardless of how functional diversity is computed, to the best of my knowledge, apart from the (extremely controversial) empirical criteria proposed by Mason *et al.* (2003), a set of basic statistical requirements that a meaningful index of functional diversity should satisfy has never been suggested.

Besides the lack of a set of meaningful statistical criteria, an additional problem with the measurement of functional diversity is that most indices do not take into account the abundance of each species. In a sense, most indices quantify just functional richness instead of functional diversity, while often some species are much more important than others in the control of ecosystem processes because of their greater abundance (Diaz and Cabido, 2001; Ricotta, 2003).

## 5. WEAK DIVERSITY MEASURES

Rao (1982) proposed a diversity index termed quadratic entropy ( $Q$ ) that reflects both species relative abundances *and* a measure of the (taxonomic or functional) pairwise species distances. Rao (1982) defined quadratic entropy as the average distance between two randomly selected individuals:

$$Q = \sum_{i,j \in \Delta} d_{ij} p_i p_j. \quad (3)$$

If  $d_{ij} = 1$  for all  $i \neq j$ , and  $d_{ii} = 0$ ,  $Q$  reduces to  $1 - D$ .

Fifteen years later, Rao's quadratic entropy was independently rediscovered by Ganeshiah *et al.* (1997) under the name "Avalanche Index" (see also Ganeshiah and Uma Shaanker, 2000).

Shimatani (2001) showed that quadratic entropy can be decomposed into three inner factors: (i) diversity of relative species abundances (computed as the Simpson index), (ii) the simple average over pairwise species distances regardless of relative species abundances, and (iii) an additional factor that embodies the 'taxonomic balance in relative species abundances' (for mathematical details, see Shimatani, 2001). Using pairwise species distances obtained from the topology of Linnaean classifications, Warwick and Clarke (1995) demonstrated a continuous decrease in the taxonomic diversity of a marine assemblage along a gradient of increasing environmental contamination in a situation where species diversity remains constant.

Despite their appealing statistical properties, it is easily shown that  $Q$  violates the usual diversity axiom that, for a given number of species  $N$ , maximal diversity arises for an equiprobable species distribution (i.e., a distribution where  $p_i = p_j = 1/N$  for all species pairs  $i \neq j$ ). Another diversity axiom that is violated by  $Q$  is the permutation invariance (Pielou 1975). This postulates that the diversity values corresponding to the relative abundances  $p_1, p_2, \dots, p_N$  and to a  $p'_1, p'_2, \dots, p'_N$  permutation of those are identical. Both axioms are a direct consequence of Dalton's principle of transfers.

An important effect of the violation of Dalton's principle of transfer is that it may happen that  $Q$  is maximized at the reduced number of species so that the disappearance of some species increases overall quadratic entropy (Shimatani, 2001). Ricotta (2002b) proposed to call these indices, that are computed from species relative abundances but that violate Dalton's principle of transfers, as 'weak diversity indices'. Some additional references on weak diversity indices are: Izsák and Szeidl (2002), and Ricotta and Avena (2003).

## 6. DISCUSSION

In this short, very selective review, I showed that there exists a clear disagreement among ecologists as far as biodiversity conceptualization and evaluation is concerned. In doing so, I deliberately emphasized the differences between the selected diversity families rather than developing any of the links between them (some references on the links between different diversity measures are: Izsák and Papp, 2000; Barker, 2002; Petchey and Gaston, 2002; Ricotta, 2002a, 2002b, 2004; Ricotta and Avena 2003). This fundamental ambiguity in the conceptualization of biological diversity renders it extremely vague as a biological concept: "Each instance, each individual property, or each species has in fact been conceived of signifying biodiversity" (Hengeveld, 1996).

Based on this premise, most readers would like to see a clear set of instructions or directions for the future of diversity as a biological concept. To the contrary, at the cost of being considered an iconoclast, I would like to stress once more that, besides very ambiguous definitions that are too indefinite to be of any universal theoretical relevance, in its very essence biodiversity measures are nothing but a set of multivariate summary statistics for quantifying different characteristics of community structure in a similar manner as similarity measures are used to quantify how closely two objects resemble each other. As emphasized by Solow and Polasky (1994): "the problem of measuring diversity can be viewed as characterizing an aspect of the distribution of points in space. It is, therefore, related to standard problems in multivariate analysis, although the aspect of interest – namely, diversity – is somewhat non-standard". This statistical part embodies the only useful aspect of the concept of biodiversity.

However, this observation should not be a cause for undue pessimism. For instance, although no one would attribute an intrinsic ecological meaning to similarity measures, nonetheless standard multivariate techniques, such as ordination or clustering methods, have been of enormous relevance for a better understanding of a large variety of ecological problems and processes. Similarly, the use of multivariate summary statistics for condensing various aspects of community structure (i.e., taxonomic, functional, structural, genetic, etc.) into a single diversity measure has proven of great importance in environmental monitoring research where the emphasis is on assessing whether sampled communities exhibit some structural changes following environmental degradation or remediation efforts, and may be equally important for relating species frequency distributions to ecosystem functions.

Obviously, the aim of this paper lies in contributing to free debate on the very nature of biological diversity, and not in suggesting an ultimate solution. In this view, an anonymous referee argued that, by extension, the same criticism on the ambiguity of the notion of biodiversity could be addressed to many biological concepts: "To take a simple example, people measure the body sizes of organisms in different ways. Any

two species may differ in body size in terms of which is larger or smaller, relative size differences, and absolute size differences, depending on the approach taken. However, biologists have not abandoned body size as a useful concept”.

Likewise, I do not say that the concept of community structure is useless. Rather, I suggest that the way in which community structure is measured is mostly a statistical problem; once community structure has been condensed into a diversity figure, its relevance to any specific ecological problem must be judged *a posteriori* on the basis of observed correlations with the selected measure of ecosystem functioning.

Also, personal communications with colleagues have elicited the point that, throughout this paper, the terms ‘biodiversity’ and ‘diversity’ are conflated, while they clearly reflect two entirely different issues. For instance, biodiversity extends far beyond species richness, abundance patterns and community structure. As stressed by Sarkar and Margules (2002): “The concept of biodiversity includes the entire biological hierarchy from molecules to ecosystems, or the entire taxonomic hierarchy from alleles to kingdoms, all the logical classes in between (individuals, genotypes, populations, species, etc.), and all of the different members of all those classes. It also includes the diversity of living interactions and processes at all these levels of organization”.

Unfortunately, this is such a wide-ranging definition that it has ensured that its measurement remains “capricious” (Sarkar and Margules, 2002). Nonetheless, to a closer look, all these capricious measures tend to reduce to a more or less sophisticated set of indices that condense various aspects of community structure into a few numbers. Thus, since different diversity measures have been defined based on distinct objectives and motivations, from an operational perspective a clear understanding of their basic properties may be beneficial for selecting (or developing) a family of measures that are most appropriate for quantifying a specific facet of community organization.

For instance, the mathematical formulation of different diversity measures can be expected to influence the sign and strength of their possible connection with the functioning and organization of biological communities. Consequently, a clear understanding of the mathematics that resides behind diversity measures is not a sterile academic exercise, or ‘scientific philately’, but an essential part of ecological research; as stressed by Hill (1973), although there is almost unlimited scope for mathematical generality in relation to diversity indices, simple measures with well-understood statistical properties should be preferably used for summarizing the structure of biological communities.

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