INTRODUCTION OF A SPECIES DOES NOT NECESSARILY INCREASE DIVERSITY

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Abstract. The notion of species diversity depends on two main components: richness of sources and the spread of items over available sources (evenness). To compare different situations a partial order is introduced into the set of all possible distributions. One such partial order is produced by the criterion of Lorenz dominance, visualized by a Lorenz curve. If a vector \mathbf{X} is diversity-dominated by a vector \mathbf{X} , the Lorenz curve of \mathbf{X} lies beneath that of \mathbf{X} . Defining the bifurcation operator BIF, we may split up an N-vector into an (N+1)-vector. Now, the Patil-Taillie bifurcation axiom, or 'introduction of a species' axiom, states that the latter vector, i.e. BIF(\mathbf{X}) must always have a larger diversity than the former. However, it may well be that the Lorenz curve of BIF(\mathbf{X}) is situated strictly beneath the Lorenz curve of \mathbf{X} . Thus, the 'introduction of a species' axiom is not comparable with the diversity-dominance order.

Lorenz curves and diversity-dominance

It is generally agreed that the notion of species diversity depends on two main components: richness of sources and the spread of items over available sources (evenness with which items are distributed among sources). Here, the words sources and items are used in a generic sense: in practical situations sources are different species and items are, e.g., abundances observed in a particular region during a specific period. Functions used to measure diversity should take these two components into account.

The number of sources will be denoted by N and a distribution of items over sources will be denoted as an N-tuple $\mathbf{X}=(x_1,...,x_N)$ where we will further assume that all $x_i>0$ (no source produces a negative number of items and all sources are non-empty). In practice, one introduces a partial order into the set of all possible distributions and requires that a diversity measure respects this partial order. The fact that this order is only a partial order means that for some pairs of distributions we can say that one is more diverse than the other, while for other pairs we suspend judgment. Usually, such a partial ordering is produced by the criterion of Lorenz dominance. Lorenz dominance depends on the use of Lorenz curves (Lorenz 1905) defined as follows.

Let $X = (x_1, x_2, ..., x_N)$ where $0 < x_1 \le x_2 \le ... \le x_N$. Then we put, for i = 1, ..., N,

$$a_{i} = \frac{x_{i}}{\sum_{j=1}^{N} x_{j}} = \frac{x_{i}}{\mu N}$$
 (1)

where μ denotes the average of the x_i . In this article a_i will always denote a relative value.

The (discrete) Lorenz curve of X, denoted as L_X , is a polygonal curve connecting the origin (0,0) with the points with coordinates

$$\left(\frac{i}{N}, \sum_{j=1}^{i} a_{j}\right), i=1,...,N.$$
 (2)

Note that

$$\sum_{j=1}^{N} a_j = 1. (3)$$

Hence the Lorenz curve ends in (1,1).

Clearly, Lorenz curves are increasing curves. As the x_i , hence also the a_i , are placed in increasing order, Lorenz curves are also convex. Practically this means that, when choosing any two different points on the curve and connecting them by a line segment, there never is a point on the curve lying above this segment.

We further note that sometimes the x_i are placed in decreasing order; in that case the Lorenz curve is concave, but we will always use the convention to order the number of items in increasing order. Fig. 1 shows the Lorenz curve of the vector (1,2,4,5) and gives an example of the convexity property.

We then say that the vector \mathbf{X} is diversity-dominated by the vector \mathbf{X} , denoted as $\mathbf{X} - \langle \mathbf{X}'$ if for every $t \in [0,1]$: $L_{\mathbf{X}}(t) \leq L_{\mathbf{X}}'(t)$. This means that the

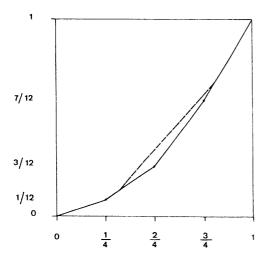


Figure 1. Lorenz curve L_X of the vector X = (1,2,4,5); the Lorenz curve is convex and every segment connecting two points of the curve (broken line) lies above the Lorenz curve.

Lorenz curve of X lies nowhere above the Lorenz curve of X'. Of course, these curves may coincide over some region. Vectors such as (1,2) and (3,6) or (1,2) and (1,1,1,2,2,2) which have the same Lorenz curve are identified and considered as equivalent from the point of view of diversity measurement. This means that diversity measures must be scale invariant. For examples of the use of Lorenz curves in ecological applications we refer the reader to Weiner and Solbrig 1984, Weiner 1985 and Eliás 1987.

We note that partial orders other than diversity-dominance, are possible.

The 'introduction of a species' property

Patil & Taillie (1982) use the property that, in the framework of their article, diversity measures satisfy the 'introduction of a species' property (Theorem 4.1). We will refer to this property as the bifurcation proper-

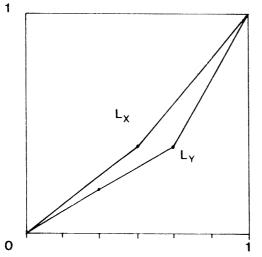


Figure 2. Lorenz curves of the vectors X = (2,3) and Y = (1,1,3).

ty and will define it using the BIFURCATION-operator BIF(i,p), where i is a number between 1 and N, and 0 .

Definition: the BIFURCATION-operator

Let $X = (x_1, x_2, ..., x_N)$ be an N-tuple. Then the BIFURCATION operator BIF(i,p) is defined as:

BIF(i,p)(X) =
$$(x_1,...,px_i,(1-p)x_i,...,x_N$$
 (4)

The resulting vector $BIF(i,p)(\mathbf{X})$ is an (N+1)-vector. The name 'introduction of a species' property refers to the interpretation that the i-th species must share a part of its resources (prey, nutrients, habitat) with a new species. The Patil-Taillie bifurcation axiom then states that if $0 , <math>BIF(i,p)(\mathbf{X})$ must have a larger diversity than \mathbf{X} . This axiom is endorsed by a number of ecologists, e.g. Swindel et al. (1984).

This bifurcation axiom, however, is not compatible with the usual diversity-dominance order. Indeed, splitting the 2-vector $\mathbf{X} = (2,3)$ may yield the 3-vector $\mathbf{Y} = (1,1,3)$. By the bifurcation axiom the latter vector should be less concentrated than the former. However, it is a fact that the Lorenz curve of (2,3) is situated strictly above the Lorenz curve of (1,1,3) (see Fig. 2).

We think that most practical ecologists would agree that the vector \mathbf{X} shows a more diverse situation than \mathbf{Y} , despite the fact that the latter contains one species more. Moreover, consider another vector $\mathbf{X} = (8,8,8,8,8,8)$. Bifurcation leads to $\mathbf{Y} = (1,7,8,8,8,8,8,8)$ which again is certainly less diverse than \mathbf{X} although the bifurcation axiom would require the converse. Actually, a diversity measure which respects the bifurcation or 'introduction of a species' axiom will always consider a situation such as (p,1-p,1,1,...,1), containing N+1 sources, as more diverse than (1,...,1), the N-sources equality situation.

We conclude that the 'introduction of a species' axiom is not a desirable property for diversity measures.

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