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On the Molinari shape of evenness measures

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SUMMARY

The degree to which abundances are divided equitably among community species or evenness is a basic property of any biological community. Several evenness indices have been proposed to summarize community structure. In addition, a number of desirable properties have been suggested that an evenness index should meet to reasonably behave in ecological research. The most basic of these properties is consistence with the Lorenz ordering. Subordinately, one additional property for an ecologically meaningful evenness index is that, in cases of two-species communities, it should keep a linear relationship between minimum and maximum evenness. It is showed here that only two evenness indices thus far proposed in ecological literature show a linear relationship between minimum and maximum evenness being at the same time consistent with the Lorenz ordering.

KEY WORDS: Gini index, Lorenz ordering, species replication.

1. Introduction

The degree of equality of species relative abundances or evenness is a basic property of any biological community. Evenness measures summarize the distribution of abundance among community species separate from any reference to named species. Maximum evenness (1.0) arises from an equiprobable species distribution, and the more that relative abundances of species differ the lower the evenness is. Several evenness indices have been proposed in the ecological literature. For a review, see Taillie (1979) and Smith & Wilson (1996). However, none seems to be generally preferred.

The concept of evenness is tightly related to that of species diversity. It is generally agreed that diversity measures combine in a non-standard way two components: species richness (the number N of community species) and evenness. High species richness and evenness are both equated with high diversity. Consequently, the foremost requirement for a meaningful evenness index is that it has to be independent of species richness. If the separation is incomplete, so that evenness is affected by species richness, then differences in evenness values could reflect differences in the species count rather than any fundamental difference in community organization (Sheldon, 1969).

To qualify for being independent of species richness, a number of authors (Hill, 1973; Taillie, 1979; Molinari, 1989; Smith and Wilson, 1996) propose that replication should not change the value of community's evenness. Imagine an N-species community characterized by the relative abundance vector $\pi = (p_1, p_2, ..., p_N)$ that such that $0 \leq p_i \leq 1$ and $\sum_{i=1}^{N} p_i = 1$. It seems reasonable that replicating the N-species sequence n-times should give a community with n-times the original species richness but the same community's evenness (Taillie, 1979). Notice that this replication property is part of Taillie's (1979) more general requirement that an evenness index maintains the natural ordering introduced by the Lorenz curves used by economists to compare wealth distributions (Routledge, 1983).

The Lorenz curve is obtained by plotting the cumulative species relative abundances as abscissa against corresponding cumulative proportions of species as ordinates (Taillie, 1979). Arrange the components of the species relative abundance vector π of a given community in descending order so that the ranked abundance vector $\pi^{\#} = (p_1^{\#}, p_2^{\#}, ..., p_N^{\#})$ is obtained, where $p_1^{\#} \geq p_2^{\#} \geq ... \geq p_N^{\#}$. The Lorenz curve is then defined as the polygonal path linking the successive points: $P_0 = (0,0)$, $P_1 = (p_1^{\#}, 1/N)$, $P_2 = (p_1^{\#} + p_2^{\#}, 2/N), ..., P_N = (p_1^{\#} + p_2^{\#} + ... + p_N^{\#}, N/N) \equiv (1,1)$ (Figure 1). The outcome is very similar to the intrinsic diversity profile proposed by Patil and Taillie (1979, 1982) for defining the concept of intrinsic diversity order: both use as abscissa the cumulative species relative abundances, however, the intrinsic diversity profile uses as ordinate the cumulative number of species, whereas the Lorenz curve uses as ordinate the cumulative proportion of species. Patil and Taillie (1979, 1982) defined community A to be intrinsically more diverse than community B without reference to indices, provided B leads to A by a finite sequence of forward transfers of abundance (for details, see Patil and Taillie, 1979, 1982). Following this definition, the hypothetical community A is intrinsically more diverse than community B if and only if community A has its intrinsic diversity profile everywhere above that of community B (Patil and Taillie, 1979, 1982). Notice that the ordering is only partial in that two communities need not necessarily be intrinsically comparable. In this latter case, the intrinsic diversity profiles of both communities cross one another. Similarly, community A is intrinsically more even than community B if and only if community A has its Lorenz curve everywhere above that of community B (Taillie, 1979). Consequently, a measure of evenness E that is invariant under species replication maintains the Lorenz ordering provided that E is consistent with the intrinsic diversity ordering when re-

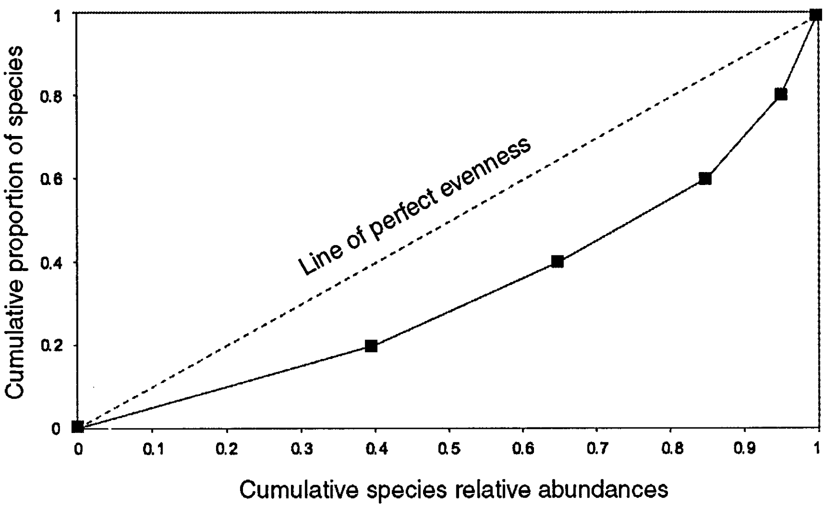

Figure 1. Lorenz curve for an artificial five-species community with relative abundances 0.40, 0.25, 0.20, 0.10, 0.05. The dotted line represents perfect evenness.

stricted to communities with the same number of species (Taillie, 1979). For instance, when diversity comparisons are restricted to communities with the same number of species, since there is no fundamental difference between diversity and evenness when species richness is held constant, the intrinsic diversity ordering is identical to the corresponding Lorenz ordering (Taillie, 1979).

2. On the Molinari shape of evenness measures

One additional criterion proposed by Molinari (1989) that an ecologically acceptable evenness index should meet is that, in cases of two-species communities, it should keep a linear relationship between minimum and maximum evenness. Allow that a given evenness measure E ranges between zero when the evenness is minimum (i.e., if there is a species having its proportional abundance approaching 1, the abundances of all other species approaching null) and unity when evenness is maximum (i.e., if $p_i = p_j$ for all species pairs $i, j = 1, 2, ..., N$). For a community composed of two species, we would assign an evenness value close to zero to the case where $p_i \to 0$ and $p_j \to 1$. Conversely, we would assign an evenness value equal to one to the case where $p_i = p_j = 0.5$. For an ideal evenness measure *sensu* Molinari (1989), because the $p_i = 0.25$; $p_j = 0.75$ case is the intermediate between the extreme cases

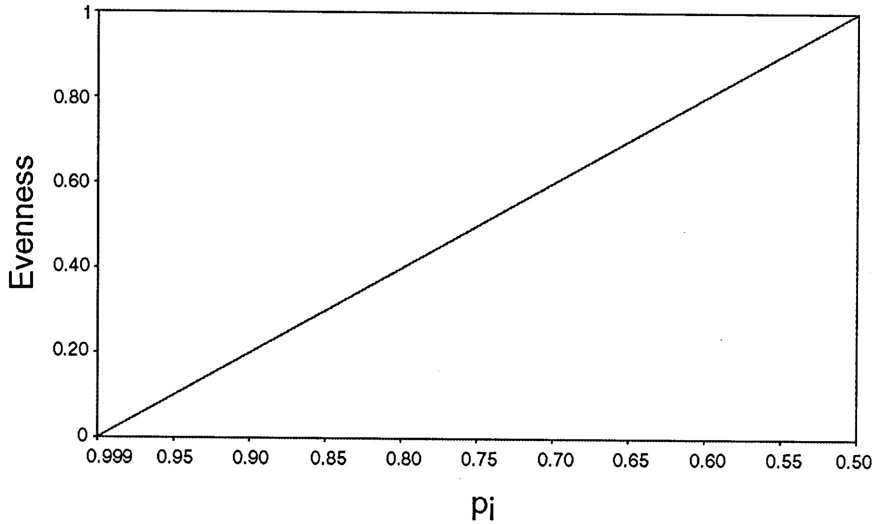

Figure 2. Evenness values for all possible abundance relationships in two-species communities for an ideal evenness measure sensu Molinari (1989)

$p_i \to 0$; $p_j \to 1$, and $p_i = p_j = 0.5$, we can assign to it the intermediate evenness value of 0.5. In the same manner, by averaging the $p_i = 0.25$; $p_j = 0.75$ and the $p_i = p_j = 0.5$ cases, we obtain the relative abundances $p_i = (0.25+0.5)/2 = 0.375$ and $p_j = (0.75+0.5)/2 = 0.625$ to which we can assign the evenness value of 0.75. Iterating this procedure, we can assign evenness values to all possible cases of two-species communities. It is worth noticing that if the values so obtained are plotted against the relative abundance p_i, the outcome is a straight line (Figure 2). Molinari (1989) further argues that, since we can know a priori the evenness values obtained from any community composed of two species, we can use two-species communities to evaluate the performance of any evenness measure intended to be later applied to species-richer communities. For instance, if we compare two multi-species communities using an evenness index with an ideal Molinari shape (i.e., with a linear response ranging from minimum evenness up to unity), it can be assumed that, since the index keeps a linear relationship to evenness, the differences obtained in the resulting values are due to actual differences in community organization, rather than to index values bearing a non-linear relationship to evenness (Molinari, 1989).

Although an ideal Molinari shape can be obtained from virtually any evenness index under a monotonic transformation, to our knowledge, among the evenness measures thus far proposed in the ecological literature, only two show an ideal Molinari shape being at the same time consistent with the Lorenz ordering. The first one is the index proposed by Bulla (1994) as

$$O = \sum_{i=1}^{N} \min(p_i, 1/N), \tag{1}$$

whereas the second one is the Gini index. If we denote the rank of the i-th component of $\pi^{\#}$ by $i^{\#}$, the Gini index, that is in fact twice the area under the Lorenz curve, is defined as (Taillie, 1979)

$$I = \left(2\sum_{i=1}^{N} i^{\#}p_i^{\#} - 1\right)/N. \tag{2}$$

Notice that I is related to Camargo's (1992) dominance index d' by the simple relation $I = 1-d'$, where $d' = \sum_{i=1}^{N}\sum_{j\geq i}^{N}\left|p_i^{\#} - p_j^{\#}\right|/N$, and $p_i^{\#}$ and $p_j^{\#}$ are the ranked relative abundances of the i-th and j-th species, respectively, so that $i^{\#} > j^{\#}$.

From the analysis of Equations (1) and (2), it is easily showen that, in the most extreme case of a very dominant species whose proportional abundance is very close to one, the minimum value assumed both by O and I tends toward $1/N$. Therefore, both indices lack the desirable property of reaching the minimum index value (i.e., zero) with any number of species. In particular, for a two-species community, $O_{min} = I_{min} = 0.5$.This shortcoming obviously cannot be solved by simple index normalization $E'(N) = (E - 1/N)/(1 - 1/N)$. For instance, following normalization, the resulting index $E'(N)$ is not invariant under species replication violating the foremost requirement for an ecologically meaningful evenness index.

3. Conclusion

Many authors (Taillie, 1979; Routledge, 1983; Molinari, 1989; Smith and Wilson, 1996) have proposed a number of desirable properties that an evenness measure should possess to reasonably behave in ecological research. However, it is generally understood that no single index can satisfy all the proposed requirements (Routledge 1983; Smith and Wilson 1996). In this paper, we suggest that, although far from perfection, the evenness measures proposed by Bulla and Gini have a number of basic properties that may render them ecologically acceptable measures of evenness. In addition, both measures are also particularly adequate in their relation to diversity. Since diversity can be informally partitioned into richness and evenness, a good evenness measure should be such that, when multiplied by the number N of community species, it will produce a meaningful index of species diversity (Bulla, 1994; Ricotta and Avena, 2000). Although this formal relation is not of universal validity, Bulla (1994) showed its validity for his evenness index O. Similarly, Rousseau et al. (1999)

showed that, as a consequence of the relation existing between the Lorenz curve and the intrinsic diversity profile, the Gini index I multiplied by the number N of community species (i.e., twice the area under the intrinsic diversity profile, also termed "adapted Gini coefficient") has several properties that render it a meaningful diversity index.

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O mierze kształtu wyrównania Molinari

STRESZCZENIE

W literaturze zaproponowano różne wskaźniki struktury populacji opisujące rozkład nadmiaru gatunków lub, inaczej, ich wyrównanie. Wskazywano, jakie własności miary wyrównania są korzystne z punktu widzenia badań ekologicznych. Najbardziej podstawową z takich własności jest zgodność z porządkiem Lorenza. Inną pożądaną włąsnością jest to, aby, w przypadku dwu gatunków, miara zachowywała liniową zależność pomiędzy minimalnym i maksymalnym wyrównaniem. W pracy pokazano, że tylko dwie z zaproponowanych miar wyrównania spełniają oba wymienione postulaty.

SŁOWA KLUCZOWE: indeks Giniego, porządek Lorenza, replikowanie gatunków.