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Unifying and distinguishing diversity ordering methods for comparing communities

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Abstract Diversity indices have been widely used in ecological research, but they remain problematic in that different indices may rank communities inconsistently. This problem can be solved by using diversity ordering methods, the output of which is a diversity profile in graphical form for each community being compared. In this paper, we demonstrate that existing diversity ordering methods can be classified into four groups and that within-group methods are essentially equivalent, while among-group methods are not. We find that the intrinsic diversity-related methods—i.e., the group containing the right tail-sum method, the logarithmic dominance plot, the majorization method, and the k-dominance plot—provide the most stringent test of diversity ordering, and we recommend the right tail-sum method as the method of preference for practical purposes.

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Introduction

Biological diversity is a central topic of interest within the field of ecology and is most frequently expressed in terms of species diversity. This term has varied meanings, the simplest being species richness, i.e. the number of species in a sample. Many diversity indices have been devised that weight both the richness and equitability (evenness of abundance) of species within samples. These are widely used in the description of community structure and in the comparison of samples or communities for environmental monitoring and conservation planning purposes (Magurran 1988, 2004). However, different diversity indices may differ in their ranking of communities (Hulbert 1971; Patil and Taillie 1982; Tóthmérész 1995); this means that the results of comparative studies are dependent upon the assumptions inherent in the selected diversity metric and that in cases where ranking differs, it is not possible to be categorical that a particular site is more diverse than another, even if the sampling regime adopted has been appropriately standardized (Kempton 1979; cf. Whittaker et al. 2001).

In view of the inadequacy of a single index, it is desirable to quantify diversity by means of diversity

profiles. A diversity profile is a curve depicting the simultaneous values of a large collection of diversity indices (Patil 2002). Instead of applying a single diversity index (such as the Shannon-Weiner index), with a particular degree of sensitivity to rare versus common species, a family of diversity indices are calculated with each member (i.e. diversity index) corresponding to a different value of a parameter. In practice, this allows the diversity of the community to be expressed with varying degrees of emphasis on rare versus common species using an otherwise standard formula. By plotting the resulting diversity profiles for two or more communities, it is then possible to determine if one community is consistently more diverse than another—i.e., its diversity values are greater than or equal to those of the other community throughout the diversity profile—in which case we may term the communities as "separable". Theoretically, this includes a special situation in which the relative abundance distributions of the communities compared are exactly the same. If this is the case, it is not necessary to use any method to rank their diversity. Should the two curves intersect, however, then one community cannot be said to be (unequivocally) more diverse than the other, and the communities are said to be "non-separable". Earlier papers on this topic (see Patil and Taillie 1982; Tóthmérész 1995) have used the term "comparable" for the situation in which a comparison can successfully be made, and one community is thus determined to be more diverse than another, and the term "non-comparable" where it is not possible to claim that one community is distinct from another with respect to its diversity. We suspect that this terminology may confuse many readers and, therefore, refer to "comparable" communities (sensu Patil and Taillie 1982) as "separable", and "non-comparable" communities as "non-separable" throughout the present paper.

This approach to diversity ordering has been used in studies across diverse sub-fields of ecology, such as range management (Lewis et al. 1988), forest management (Gove et al. 1995; Solomon and Gove 1999), plant community ecology (Ricotta et al. 2002, 2003), and macrobenthic community ecology (Kandall and Aschan 1993).

We can express the fundamentals of the diversity ordering method mathematically as follows. A parametric family of diversity indices takes the form $\{D_\alpha : \alpha \in F\}$, where D_α represents the diversity index for a given value of the parameter α, and F contains either a finite or an infinite number of real numbers (depending on the family of diversity indices chosen). If, and only if, the values of D_α for Community A for each value of

α are greater than or equal to those for Community B, is it correct to state that Community A is more diverse than Community B, which is denoted as $A \succ B$ (Tóthmérész 1995).

Intuitively, the approach of using a family of diversity indices is better than just using one or a few diversity indices, especially when we are interested in comparing the diversity of different communities. This is the starting point of the diversity ordering approach. However, since diversity is a multi-dimensional phenomenon, theoretically it is possible to derive many parametric families of indices for diversity ordering (e.g. Rényi's generalized entropy and the right tail-sum method). Unfortunately, these methods in turn differ from one another and can therefore produce conflicting results. Consequently, it is important to establish how these ordering methods compare to one another so that ecologists can make appropriate use of them.

A useful contribution to this problem was made by Tóthmérész (1995), who compared the performance of 12 diversity ordering methods, but who failed to provide a fully developed classification of the methods. In the present paper, we build on this starting point, in the hope that clarification of the similarities and differences among these diversity ordering methods will encourage the appropriate use of the techniques currently available in some software packages [e.g. SPECIES DIVERSITY & RICHNESS III (http://www.pisces-conservation.com/demos/SDRInstructions.pdf), PAST (PAlaeontological STatistics, ver. 1.52, http://www.folk.uio.no/ohammer/past/), and VEGAN (Community Ecology Package, ver.1.8-2, http://www.rss.acs.unt.edu/Rdoc/library/vegan/html/00Index.html)] and the inclusion of the methods in other software packages for ecologists [e.g. BIODIV (ver. 5.1, http://www.exeter-software.com/cat/biodiv.html), SPADE (Species Prediction And Diversity Estimation, http://www.chao.stat.nthu.edu.tw/softwareCE.html), and ESTIMATES (Statistical estimation of species richness and shared species from samples, ver. 7.5, http://www.viceroy.eeb.uconn.edu/estimates)].

In this paper, we show that the existing diversity ordering methods can be classified into four groups (Table 1) and that within-group methods are equivalent, whereas methods drawn from different groups are not equivalent. The equivalence of within-group methods is to be demonstrated mathematically, and the non-equivalence of among-group methods is to be demonstrated by real communities from published literature. We consider the performance of the different groups and offer a recommendation that the intrinsic diversity-related methods provide the most stringent tests of diversity ordering.

Table 1 Methods for diversity ordering

No.	Name	Formula[a]	Special cases[a]	Reference
Group 1: Information-related methods				
1.	Rényi's generalized entropy	$H_\alpha = \left[\ln\left(\sum_{i=1}^{S} p_i^\alpha\right)\right] \Big/ (1-\alpha)$ $(\alpha \geq 0, \alpha \neq 1)$	$H_0 = \ln S, H_1 = H'$ $H_2 = -\ln SD, H_\infty = -\ln p_{[1]}$	Tóthmérész (1995)
2.	Hill's diversity number of order a	$N_a = \left(\sum_{i=1}^{S} p_i^a\right)^{1/(1-a)}$ $(a \geq 0, a \neq 1)$	$N_0 = S, N_1 = \exp(H')$ $N_2 = 1/SD, N_\infty = 1/p_{[1]}$	Hill (1973)
3.	Daróczy's entropy of type α	$H^{(\alpha)} = \left(\sum_{i=1}^{S} p_i^\alpha - 1\right) \Big/ (2^{1-\alpha} - 1)$ $(\alpha \geq 0, \alpha \neq 1)$	$H^{(0)} = S - 1, H^{(1)} = H'/\ln 2$ $H^{(2)} = 2(1-SD), H^{(\infty)} = 1$	Daróczy (1970)
4.	Numbers equivalent	$S_\beta = \left(\sum_{i=1}^{S} p_i^{\beta+1}\right)^{-1/\beta}$ $(\beta \geq -1, \beta \neq 0)$	$S_{-1} = S, S_0 = \exp(H')$ $S_1 = 1/SD, S_\infty = 1/p_{[1]}$	Patil and Taillie (1979, 1982)
5.	Diversity index of degree β	$\Delta_\beta = \left(1 - \sum_{i=1}^{S} p_i^{\beta+1}\right) \Big/ \beta$ $(\beta \geq -1, \beta \neq 0)$	$\Delta_{-1} = S - 1, \Delta_0 = H'$ $\Delta_1 = 1 - SD, \Delta_\infty = 0$	Patil and Taillie (1979, 1982)
6.	Tsallis' generalized entropy	$H_q^T = \left(1 - \sum_{i=1}^{S} p_i^q\right) \Big/ (q-1)$ $(q \geq 0, q \neq 1)$	$H_0^T = S - 1, H_1^T = H'$ $H_2^T = 1 - SD, H_\infty^T = 0$	Tsallis (2002)
Group 2: Expected number of species-related methods				
7.	Hulbert's family of diversity index	$s(m) = \sum_{i=1}^{S}[1 - (1-p_i)^m]$ $(m \geq 1)$	$s(1) = 1, s(\infty) = S$ $s(2) = (1-SD) + 1$	Hulbert (1971)
8.	Hurlbert-Smith-Grassle index of order ω	$\Delta_\omega^{\mathrm{HSG}} = \sum_{i=1}^{S}(1-p_i)[1-(1-p_i)^\omega]$ $(\omega \geq 0)$	$\Delta_0^{\mathrm{HSG}} = 0, \Delta_1^{\mathrm{HSG}} = 1 - SD$ $\Delta_\infty^{\mathrm{HSG}} = S - 1$	Patil and Taillie (1979)
Group 3: Rank-type index-related method				
9.	Rank-type index	$\Delta_\rho^{(\mathrm{rank})} = \sum_{i=1}^{S}\left(1 - \sum_{j=1}^{i} p_{[j]}\right)\rho^{i-1}$ $(\rho \geq 0)$	$\Delta_0^{(\mathrm{rank})} = 1 - p_{[1]}$	Patil and Taillie (1982)
Group 4: Intrinsic diversity-related methods				
10.	Right tail-sum method	$(i, T_i) = \left(i, \sum_{j=i+1}^{S} p_{[j]}\right)$ $(i = 1, 2, ..., S-1)$	$(0, T_0) = (0,1), (S, T_S) = (S, 0)$	Patil and Taillie (1979, 1982)
11.	Logarithmic dominance plot	$(\log i, L_i) = \left(\log i, \sum_{j=i+1}^{S} p_{[j]}\right)$ $(i = 1, 2, ..., S-1)$	$(\log S, L_S) = (\log S, 0)$	Tóthmérész (1995)
12.	Majorization method	$(i, M_i) = \left(i, \sum_{j=1}^{i} p_{[j]}\right)$ $(i = 1, 2, ..., S)$		Solomon (1979)
13.	k-dominance plot	$(\log i, k_i) = \left(\log i, 100 \cdot \sum_{j=1}^{i} p_{[j]}\right)$ $(i = 1, 2, ..., S)$		Shaw et al. (1983)

[a] S is the number of species in a community, $(p_1, p_2, ..., p_S)$ is the relative abundance of the S species, and $(p_{[1]}, p_{[2]}, ..., p_{[S]})$ is that distribution arranged in descending order. For the methods in Group 4, the diversity profile is defined by the polygonal path joining successive points. $H' = -\sum_{i=1}^{S} p_i \ln p_i$ is the Shannon-Wiener diversity index calculated with the natural logarithm. $SD = \sum_{i=1}^{S} p_i^2$ is Simpson's dominance index. H_∞ is the limit of H_α when α tends to infinity. Other notations ($N_\infty, H^{(\infty)}, S_\infty, \Delta_\infty, H_\infty^T, s(\infty)$ and $\Delta_\infty^{\mathrm{HSG}}$) should be understood in a similar way.

The consistency of within-group methods

The method names, formulae, and an appropriate source reference are given in Table 1, in which we have also grouped the methods into the four groups: *information*-related methods (Group 1), *expected number of species*-related methods (Group 2), *rank-type index*-related methods (Group 3), and *intrinsic diversity*-related methods (Group 4). First, we show that the six methods in Group 1 are closely related and consistent

in ranking communities. In fact, after changing parameters in the other Group 1 methods, these families of indices can be written as some form of exponential function of Rényi's generalized entropy (either $\exp(H_\alpha)$ or $\{\exp[(1-\alpha)H_\alpha] - 1\}/(2^{1-\alpha} - 1)$ or $\{\exp[(1-\alpha)H_\alpha] - 1\}/(1-\alpha)$), and these functions are all strictly monotonically increasing functions of H_α ($\alpha \geq 0$) (See Appendix 1 for detailed mathematical demonstration). Consequently, they rank communities consistently. In this respect, these six methods are

equivalent in their ordering of the communities being compared.

Second, we consider Group 2 (*expected number of species*-related methods), which consists of Hulbert's family of diversity index and Hurlbert-Smith-Grassle index of order ω. Consider

$$\Delta_\omega^{\mathrm{HSG}} = s(\omega + 1) - 1. \tag{1}$$

If we transform the parameter $\omega + 1$ to m, it is clear that there is only a difference of 1 between the two methods. When ω is an integer, the Hurlbert-Smith-Grassle index of order ω is one less than the expected number of species obtained when $\omega + 1$ individuals are randomly selected from the community (Patil and Taillie 1979). Therefore, they are equivalent in ranking communities.

In addition, a minimum variance unbiased estimator exists for Hulbert's family of diversity indices (Smith and Grassle 1977):

$$\widehat{s}(m) = \sum_{i=1}^{S} \left\{ 1 - \binom{N - n_i}{m} \middle/ \binom{N}{m} \right\}, \tag{2}$$

where $\binom{N}{m} = \frac{N!}{(N-m)!m!}$, n_i $(i = 1, 2, \ldots, S)$ is the number of individuals for species i among the m individuals randomly drawn from the total number of N individuals.

Since there is no such counterpart for many of the other methods, the sampling properties among the methods will not be compared in this paper. For those readers who are interested in the statistical issues relevant to diversity measurement, please refer to Smith and Grassle (1977), Tong (1983), Fattorini and Marcheselli (1999), Gotelli and Colwell (2001), Patil (2002), Colwell et al. (2004), Di Battista and Gattone (2004). In the latter part of this paper, we assume that the data we are concerned with represent whole communities and not samples of them, therefore, rather than Eq. (2), the formulas in Table 1 will be used. However, when only Hulbert's family of diversity indices is selected and individuals for each species are sampled from a community, then Eq. (2) instead of the formulas in Table 1 should be used to construct the diversity profile.

Group 3 (*rank-type index*-related method) consists of a single method, the rank-type index-related method $\Delta_\rho^{(\mathrm{rank})}$, proposed by Patil and Taillie (1982). This method is distinct from the other methods, as shown in the next section.

Group 4 (*intrinsic diversity*-related methods) comprises four methods: the right tail-sum method, the logarithmic dominance plot, the majorization method,

and the k-dominance plot. Patil and Taillie's (1979, 1982) right tail-sum method and the logarithmic dominance plot of Tóthmérész (1995) are equivalent since the only difference is that the x-coordinates are log-transformed in the latter. Solomon's (1979) majorization method and the k-dominance plot proposed by Shaw et al. (1983) are also equivalent since the x-coordinates are only log-transformed and the y-coordinates are positively linearly transformed in the latter. Actually, these two methods directly rank dominance rather than diversity. However, because the right tail-sum statistic ($\sum_{j=i+1}^{S} p_{[j]}$, $i = 1, 2, \ldots, S - 1$, where $p_{[j]}$ is the relative abundance of the j-th most abundant species (a convention followed throughout this paper), was used in the right tail-sum method and the logarithmic dominance plot and because the left tail-sum statistic $\left(\sum_{j=1}^{i} p_{[j]}, \ i = 1, 2, \ldots, S - 1 \right)$ was used in the other two methods in the group, the right tail-sum statistic and the left tail-sum statistic are exactly complementary, and the majorization method and the k-dominance plot will give the same result in ranking the diversity of communities as the other two methods. The equivalence of the right tail-sum method and majorization method was also demonstrated by Patil and Taillie (1979, 1982). Therefore, the results of all the four methods in Group 4 are consistent with each other.

Tóthmérész (1995) also listed the Lorenz curve

$$(P_0, 0) = (0, 0), (P_i, i/S)$$
$$= \left(\sum_{j=1}^{i} p_{[j]}, i/S \right) \quad (i = 1, 2, \ldots, S) \tag{3}$$

as a diversity profile. In fact, the Lorenz curve characterizes the evenness of communities (Taillie 1979; Rousseau et al. 1999). When the number of species is the same for all of the communities compared, this method is equivalent to the above four methods (i.e. Group 4 methods). Alternatively, if we take the S in Eq. (3) as the maximum value of the number of species among all the communities compared, the result is also equivalent to those of the above four methods. However, this is not the original meaning of the method.

The inconsistency of among-group methods

In this section, we will show the inconsistency among the methods from different groups using two examples with published data. Since within-group methods are consistent with each other, we will use Rényi's generalized entropy (H_α), Hulbert's family of diversity index

$(s(m))$, Patil and Taillie's rank-type index ($\Delta_\rho^{(rank)}$), and the right tail-sum method (T_i) as representatives of the methods in Groups 1, 2, 3 and 4 respectively.

For the first example, we use data provided by Magurran (1988, p. 156) for four communities (C1–C4) in the form of the number of individuals for various species as food items in flounder stomachs from four different stations (Table 2). The results of the comparisons for two pairs of communities (C1 and C2, and C3 and C4) using the above-mentioned four methods are shown in Fig. 1. It can be seen that the pair C1 and C2 are considered as separable (i.e., one can be stated to be unequivocally more diverse than another; here, C2 is more diverse than C1) by Group 1 methods and as non-separable (i.e., one cannot be stated to be unequivocally more diverse than another) by the other three groups. In contrast, the pair C3 and C4 are considered as separable (C3 is more diverse than C4) by Group 1 and Group 3 methods and as non-separable by the other two groups. Therefore, the results of the pair C1 and C2 demonstrate the inconsistency between Group 1 and Group 2, Group 1 and Group 3, and Group 1 and Group 4, while the results of the pair C3 and C4 demonstrate the inconsistency between Group 2 and Group 3, and Group 3 and Group 4 as well as others.

In our second example, we demonstrate the inconsistency between Group 2 and Group 4 using the data for three communities taken from Magurran (1988, p. 158), which include the number of individuals for various fish species in three sections of the Upper Region of Black Creek, Mississippi (Table 3). The results of the comparisons for three pairs of communities (C5 and C6, C5 and C7 and C6 and C7) using the

above-mentioned four methods are shown in Fig. 2. It can be seen that the community pair C5 and C6 are considered to be non-separable by the Group 4 method and as separable by the other groups of methods, the community pair C5 and C7 are considered to be separable by all the four groups of methods, and the community pair C6 and C7 are considered to be non-separable by all four groups of methods. Therefore, the results of the community pair C5 and C6 demonstrate the inconsistency between Group 2 and Group 4 methods as well as others.

From these two examples, we can see the general pattern: (1) if two communities are separable (i.e., one can be stated to be unequivocally more diverse than another) according to the methods in Group 4, they are also separable according to the other three groups of methods (e.g., C5 and C7); (2) if a pair of communities are non-separable according to the methods in Group 4, they may be either separable or non-separable according to the other group(s) of methods (e.g., C1 and C2, and C3 and C4). In particular, even if communities are separable with all three groups of methods (Group 1, Group 2. and Group 3), they may still be non-separable according to the methods in Group 4 (e.g., C5 and C6). Furthermore, if a pair of communities are non-separable by any of the three groups (Groups 1–3), they must also be non-separable by Group 4 methods. In this sense, the methods in Group 4 are more stringent (more conservative) than the methods in the other groups.

However, how common is the among-group inconsistency in real studies? To answer this question we compiled three datasets from published literature, including a set of insect count data from Janzen (1973), a set of bird count data from Lack and Venables (1939), and a set of data on various communities from different sources (See Appendix 2 for details on the data). For these datasets, we used the four above-mentioned representative methods and only compared the communities in the same original study, using the same sampling method and the same abundance measure (e.g., number of individuals, biomass, coverage, importance, etc.). The number of communities, number of pairs of communities compared, and comparison results for each dataset and for a combination of all the three datasets are shown in Table 4.
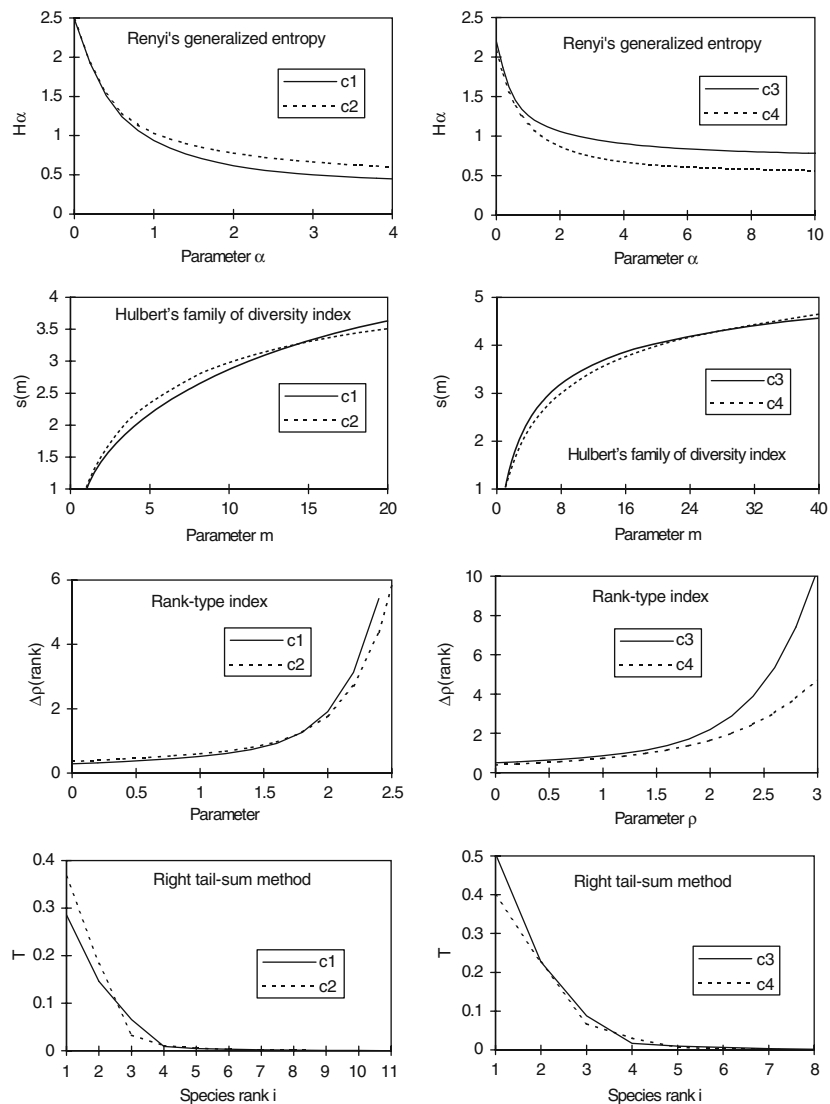
It can be seen that a consistent pattern exists among different datasets. The largest inconsistency occurs between Group 2 and Group 4 methods, for which the inconsistent cases account for more than 10% of the cases for dataset ''Bird'' and ''Mixed'' and the ''Combined'' dataset; this is followed by Group 1 and Group 2, Group 2 and Group 3, Group 1 and Group 4, and

Table 2 The number of individuals of each species in the stomachs of flounder (*Platichthys flesus*) at four sampling stations (C1–C4)[a] in the estuary of the River Bann, Northern Ireland (Magurran 1988, p. 156)

Species rank	Number of individuals of each species			
	C1	C2	C3	C4
1	3487	5681	320	436
2	683	1642	180	126
3	394	1348	90	115
4	275	196	46	27
5	22	48	5	17
6	8	21	2	3
7	6	12	2	1
8	4	7	1	1
9	2	5	1	
10	1	3		
11	1	1		
12	1	1		

[a] The four stations are considered to be four communities

Fig. 1 Diversity profiles for the four communities (C1–C4, for which the species abundances are listed in Table 2) calculated from four methods, including Rényi's generalized entropy (H_α), Hulbert's family of diversity indices ($s(m)$), Patil and Taillie's rank-type index ($\Delta_\rho^{(rank)}$), and the right tail-sum method (T_i), which are considered to be representative of the four groups of methods, respectively

Group 3 and Group 4. The least inconsistency occurs between Group 1 and Group 3, for which the inconsistent cases account for about 3% of comparisons for the dataset "Mixed" and less than 2% for the "Combined" dataset. When Group 4 is compared to all of the other three groups, the inconsistent cases account for more than 11% for the dataset "Bird" and the "Combined" dataset and more than 15% for the dataset "Mixed".

Another general pattern exists among different datasets. The highest number of pairs of communities are considered to be separable by Group 2 methods (about 68–81% for different datasets), followed by Group 1 methods (about 65–78%), Group 3 methods (about 62–77%), and finally Group 4 (about 56–75%). This result also shows that more than half of the pairs of communities are separable by any of these diversity ordering methods.

Discussion and conclusion

The inconsistency we have demonstrated here between the methods in Group 4 (*intrinsic diversity*-related methods) and some methods in other groups can be inferred from Patil and Taillie's (1979, 1982) work. To discuss this within the proper context, it is first necessary to introduce their definition of the concept of intrinsic diversity. Community c' is defined to be intrinsically more diverse than community c if it can be derived from c by a sequence of three operations: (1) introducing a new species to share the abundance with a species already present; (2) transferring abundance between two species to make them more equivalent (see also Kempton 1979, 2002); (3) permuting the abundance of the components of the abundance vector. According to Patil and Taillie (1979, 1982), community c' is intrinsically more diverse than community c if, and

Table 3 The number of individuals of each fish species in three sections (C5–CR)[a] of the Upper Region of Black Creek, Mississippi (Magurran 1988, p. 158)

Species rank	Number of individuals of each fish species		
	C5	C6	C7
1	1827	918	945
2	749	330	312
3	585	205	190
4	281	123	122
5	179	77	67
6	145	72	51
7	140	56	46
8	104	56	36
9	78	54	31
10	60	52	30
11	57	38	19
12	56	34	15
13	43	33	12
14	39	11	10
15	38	5	9
16	26	4	7
17	23	4	5
18	23	1	4
19	20	1	4
20	13		3
21	7		1
22	4		1
23	4		
24	3		

[a] The three sections are considered to be the three communities

only if, $T_i(c') \geq T_i(c)$, $i = 0,1,2, ..., S$, where T_i is the right tail-sum diversity (i.e., the first method in Group 4). They further stated that a family of indices D can be termed complete if community c' is intrinsically more diverse than community c when $D(c') \geq D(c)$ for all indices D in the family. They noticed that $\{\Delta_\beta : \beta \geq -1\}$ (i.e., diversity index of degree β) is not complete and $\{\Delta_\rho^{(\text{rank})} : \rho \geq 0\}$ (i.e. *Rank-type index*-related method) is complete for three-species communities (this fails for more than three species, however). They also stated that there are communities that are consistently ordered by the entire family $\{\Delta_\beta : \beta \geq -1\}$ (i.e., the diversity index of degree β) even though they are not intrinsically separable. This means that even when communities are separable with these two families of diversity indices $\{\Delta_\beta : \beta \geq -1\}$ and $\{\Delta_\rho^{(\text{rank})} : \rho \geq 0\}$ (Groups 1 and 3, respectively), they may still be non-separable with the last group of methods. Patil (2002) further stated that "The Δ_β profiles are isotonic to intrinsic diversity ordering in that, if an intrinsic diversity ordering exists, they will preserve it. However, the Δ_β profiles may not cross even if the T_i profiles do; therefore, the Δ_β profiles do not necessarily reflect intrinsic diversity ordering. Since the diversity indices discussed have the

same properties as the Δ_β profiles, it should be emphasized that, of the methods presented thus far, the T_i profiles are the most reliable measure of intrinsic diversity ordering between communities." Our example shows that even when communities are separable with all the first three groups of methods (*information*-related, *expected number of species*-related, and *rank-type index*-related methods), they may still be non-separable with the last group of methods (Group 4, *intrinsic diversity*-related methods).

It has also been proved that if a function $f(p_1, p_2, ..., p_S)$ is Schur concave, i.e.

$$\left(\frac{\partial f}{\partial p_i} - \frac{\partial f}{\partial p_j}\right)(p_i - p_j) \leqslant 0 \ (i, j = 1, 2, \ldots, S),$$

then it will preserve the ordering whenever there is an intrinsic diversity ordering between two communities (Kempton 1979, 2002; Tong 1983). It can be shown that all of the functions (except the Majorization method and the K-dominance plot, which are essentially the complement of the right tail-sum diversity) in Table 1 as well as many other commonly used diversity measures (see Kempton 1979, 2002; Tong 1983) are Schur concave. Therefore, all of the methods in Table 1 will give identical orderings if intrinsic diversity ordering exists; in other words, when two communities are separable by the Group 4 methods, they are also separable by the other methods. This can be seen from our results of C5 and C7. However, when two communities are not intrinsically separable, the results are unpredictable for the other methods (e.g., the results of C1 and C2, C3 and C4). Therefore, we hold that the condition of separability as shown by the methods in Group 4 is the strongest—i.e., they provide the most stringent test of diversity ordering.

Since the parameters in the diversity families are defined in such a way that they may go to infinity (for Groups 1, 2 and 3), if the indices are only calculated using a limited range of the parameters, the intersections in their diversity profiles may not be detected. In our second example, that for Hulbert's family of diversity indices, a method in Group 2, the profiles for C6 and C7 cross at $m = 126.15$ (see Fig. 2). If the indices are only calculated for smaller values of the parameter, this intersection may not be detected. If so, an incorrect conclusion will be made that the two communities (C6 and C7) are separable. Patil (2002) stated that calculating and plotting Δ_β profiles (i.e., diversity index of degree β) for $\beta > 1$ might not be helpful because either the profiles tend to converge quickly beyond this point or intersections do not resolve.

Fig. 2 Diversity profiles for the three communities (C5–C6, for which the species abundances are listed in Table 3) calculated from four methods, Rényi's generalized entropy (H_α), Hulbert's family of diversity indices ($s(m)$), Patil and Taillie's rank-type index ($\Delta_\rho^{(rank)}$), and the right tail-sum method (T_i), which are considered to be representative of the four groups of methods, respectively
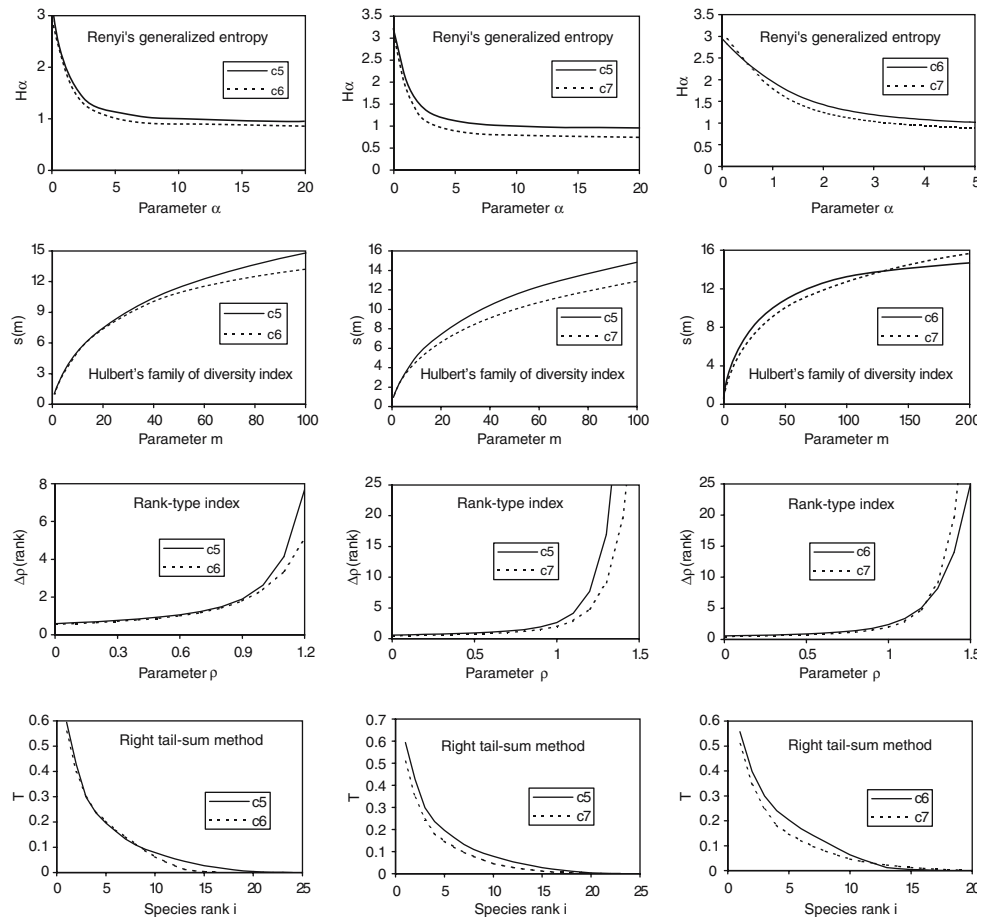

Table 4 Comparison results for three sets of real data and the combination of the three datasets (see Appendix 2 for a detailed description of the data)

Dataset	NC[a]	NPCC[b]	G1C[c]	G2C[c]	G3C[c]	G4C[c]	G1v2[c]	G1v3[d]	G1v4[d]	G2v3[d]	G2v4[d]	G3v4[d]	G123v4[e]	Source of data
Insect	168	5,944	77.46	80.48	76.85	74.44	5.15	1.14	3.01	4.95	6.04	2.41	7.37	Janzen (1973)
Bird	274	3,7401	74.41	80.73	73.16	70.01	8.51	1.41	4.39	7.86	10.71	3.14	11.84	Lack and Venables (1939)
Mixed	375	2,222	65.21	68.50	62.65	56.48	10.49	3.02	8.73	9.18	12.02	6.17	15.84	See Appendix 1
Combined	817	45,567	74.36	80.10	73.13	69.93	8.17	1.46	4.42	7.54	10.17	3.19	11.23	

[a] NC, Total number communities in the dataset

[b] NPCC, Total number of pairs of communities compared

[c] G1C, G2C, G3C, and G4C are the percentage number of pairs of communities identified as separable by Group 1, Group 2, Group 3 and Group 4 methods, respectively. The numbers from the column G1C to column G123v4 are presented as the percentage number of NPCC

[d] G1v2 through G3v4 are the percentage number of pairs of communities that are inconsistently ranked by Group 1 and Group 2, Group 1 and Group 3, Group 1 and Group 4, Group 2 and Group 3, Group 2 and Group 4, and Group 3 and Group 4 methods

[e] G123v4 is the percentage number of pairs of communities that are inconsistently ranked by Group 4 and any of the other three groups of methods

With reference to the ease of graphically comparing diversity among communities, Tóthmérész (1995) argued in favor of one Group 1 and one Group 4 method (Rényi's generalized entropy and logarithmic domi-nance plot, respectively) as the most useful methods for communities of all sizes, recommending another Group 4 method, the right tail-sum, only for small communities. However, we suggest that the right

tail-sum method should be the first choice in ranking the diversity of communities. In this aspect, we support Patil (2002) who suggested that ... "Perhaps the most useful way to compare diversity between communities is by the concept of intrinsic diversity ordering." The first reason for this is that the condition of diversity separability for this method is the strongest: i.e., when communities are detected to be separable (distinguishable into a rank diversity series) with this method, they are also separable with all the other methods, whereas the reverse may not apply. Moreover, this method (and also the other methods in Group 4) is the most reliable for the intrinsic diversity ordering of communities (Patil 2002). The second reason is that only a finite number of values (one less than the number of species) need to be calculated (only by addition) and compared, and even if graphical detection of intersections is difficult because the profiles of diversity of the communities are close to each other in some parts, a limited number of direct numerical comparisons can easily be undertaken.

There have been relatively few studies published on diversity ordering. Sufficient and necessary conditions for intrinsic diversity have been established for communities in which the species abundance distributions follow either the log-normal or the log-series distributions (see Patil and Taillie 1979; Kempton 2002), but the conditions are not known for other types of communities. Our study has served to identify four groups of diversity ordering methods between which inconsistency may occur, but we still do not know the conditions under which the inconsistency will occur among the methods. Since our sample size is not very large and the samples are not very representative (because we did not draw them systematically from the literature), we cannot definitely say how often this inconsistency is likely to occur. However, that inconsistencies occur in more than 10% of the pairs of communities examined suggests that the rate of inconsistency is non-trivial.

There are some other approaches to diversity ordering. In addition to intrinsic diversity ordering and the Lorenz curve (for evenness ordering), Rousseau et al. (1999) proposed four other partial orders for diversity and evenness ordering that are based on, or adapted from, the Lorenz curve. These researchers also concluded that intrinsic diversity ordering is the most rigorous of the six they studied. Mosler (2001) proposed a multi-dimensional approach to diversity and evenness ordering. Unlike the traditional approach to diversity measurement, whereby the species can only have one attribute (e.g., a measure of abundance, such as the number of individuals, or biomass, or cover), in a multivariate approach, the species can have more than one attribute. However, these new approaches have yet to be applied in real situations. The difficulty in interpretation and in computation, especially for the latter approach, will likely provide barriers to their application. Given this, we recommend intrinsic diversity ordering for wider application, evaluation and development within the field of ecology.

Appendix 1: The consistency of methods within Group 1

In fact, through simple mathematical manipulation [including changing a to α in Hill's diversity number of order a, transforming $\beta + 1$ to α in Patil and Taillie's (1982) numbers equivalent and diversity index of degree β, and changing q to α in Tsallis' (2002) generalized entropy], we can derive the following equations:

$$N_a = \exp(H_\alpha) \ (\alpha \geq 0, \alpha \neq 1, a \geq 0, a \neq 1)$$
$$\text{and} \quad N_1 = \exp(H_1), \tag{4}$$

$$S_\beta = \exp(H_\alpha) \ (\alpha \geq 0, \alpha \neq 1, \beta \geq -1, \beta \neq 0)$$
$$\text{and} \quad S_0 = \exp(H_1), \tag{5}$$

$$H^{(\alpha)} = \{\exp[(1-\alpha)H_\alpha] - 1\}/(2^{1-\alpha} - 1) \ (\alpha \geq 0, \alpha \neq 1)$$
$$\text{and} \quad H^{(1)} = H_1/\ln 2, \tag{6}$$

$$\Delta_\beta = \{\exp[(1-\alpha)H_\alpha] - 1\}/(1-\alpha)$$
$$(\alpha \geq 0, \alpha \neq 1, \beta \geq -1, \beta \neq 0) \text{ and } \Delta_0 = H_1, \tag{7}$$

$$H_q^T = \{\exp[(1-\alpha)H_\alpha] - 1\}/(1-\alpha)$$
$$(\alpha \geq 0, \alpha \neq 1, q \geq 0, q \neq 1) \text{ and } H_1^T = H_1 \tag{8}$$

where, $H_1 = H' = -\sum_{i=1}^S p_i \ln p_i$. Further mathematical manipulations show that $\exp(x)$, $\{\exp[(1-\alpha)x] - 1\}/(2^{1-\alpha} - 1)$ and $\{\exp[(1-\alpha)x] - 1\}/(1-\alpha)$ are all strictly monotonically increasing functions of x. Therefore, $N_a(a \geq 0), S_\beta(\beta \geq -1), H^{(\alpha)}(\alpha \geq 0), \Delta_\beta$ $(\beta \geq -1)$ and $H_q^T (q \geq 0)$ are all strictly monotonically increasing functions of $H_\alpha \ (\alpha \geq 0)$ for each specific parameter and the corresponding transformation.

Appendix 2

Table 5 Description for the data used in Table 4

Community	Habitat	Location	Samples	C[a]	Abundance	Reference
Dataset: Insect						
Beetle	Various tropical habitat	Costa Rica, Caribbean Islands	Sweep	78	Count	Janzen (1973)
Bug	Various tropical habitat	Costa Rica, Caribbean Islands	Sweep	76	Count	Janzen (1973)
Arthropod	Various tropical habitat	Costa Rica, Caribbean Islands	Sweep	14	Count	Janzen (1973)
Dataset: Bird						
Bird	Woodland	Britain	Unknown	219	Count	Lack and Venables (1939)
Dataset: Mixed						
Zooplankton	Reservoir	Tanzania	Plankton net	8	Percent count	Bailey (1978a)
Macroinvertebrate	Reservoir	Tanzania	Pond net	7	Percent count	Bailey (1978a)
Macroinvertebrate	Reservoir	Tanzania	Pond net	7	Percent weight	Bailey (1978a)
Fish	Reservoir	Tanzania	Net	6	Count	Bailey (1978b)
Fish	Reservoir	Tanzania	Net	6	Weight	Bailey (1978b)
Snake	Various habitat	Panama	Unknown	18	Count	Dun (1949)
Macrobenthic fauna	Marine	Scotland	Grab	11	Count	Pearson (1975)
Macrobenthic fauna	Marine	Scotland	Grab	11	Weight	Pearson (1975)
Macrobenthic fauna	Marine	Scotland	Grab	11	Count	Pearson (1975)
Macrobenthic fauna	Marine	Scotland	Grab	11	Weight	Pearson (1975)
Plant	Grassland	Japan	Quadrat	21	Dominance	Takatsuki (1980)
Tree	Forest	Japan	Quadrat	2	Density	Takatsuki (1980)
Tree	Urban and suburban	Korea	Districts	13	Count	Kang et al. (1984)
Plant	Subalpine forest	Japan	Quadrat	19	Dominance	Tsuda (1985)
Tree	Urban and suburban	Korea, Japan	Districts	6	Count	Kang et al. (1985)
Tree	Forest	Japan	Quadrat	5	Density	Takehara (1989)
Tree	Forest	Japan	Quadrat	5	Basal area	Takehara (1989)
Arthropod	Reclaimed land	Korea	Cylindrical sampler	9	Count	Yoshida et al. (1989)
Oribatid	Reclaimed land	Korea	Cylindrical sampler	6	Count	Yoshida et al. (1989)
Woody plant	Greenhouse	Japan	Unknown	4	Count	Hirabuki (1988)
Plant	Post-fire forest	Japan	Quadrat	14	Biomass	Kikuchi et al. (1987)
Plant	Forest	Japan	Unknown	10	Cover	Hara (1987)
Mangrove	Mangrove forest	Philippines	Unknown	15	Cover	Mochida et al. (1994)
Plant	Mire	Japan	Quadrat	18	Frequency	Sato and Miura (1996)
Plant	Degraded forest	Pakistan	Quadrat	6	Importance	Hussain et al. (1997)
Fish	Shallow bay	California, USA	Unknown	4	Count	Molles (1978)
Invertebrate	Stream	Oregon, USA	Surber sampler	10	Count	Hawkins et al. (1982)
Invertebrate	Stream	Oregon, USA	Surber sampler	9	Count	Hawkins et al. (1982)
Invertebrate	Stream	Oregon, USA	Surber sampler	10	Biomass	Hawkins et al. (1982)
Microarthropod	Old fields	S. Carolina, USA	Litterbag	9	Count	Wiegert (1974)
Microarthropod	Road margin	Chicago, USA	Soil core	18	Count	Lussenhop (1973)
Marsh plant	River delta	Mississippi, USA	Line-intercept	6	Percent cover	Chabreck and Palmisano (1973)
Bat	Various habitat	Panama and Costa Rica	Net	3	Count	Fleming et al. (1972)
Bird	Plantation	Britain	Unknown	17	Percent count	David (1939)
Bird	Plantation	Britain	Unknown	7	Count	David (1939)

Table 5 Continued

Community	Habitat	Location	Samples	C[a]	Abundance	Reference
Bird	Farmland	Britain	Unknown	24	Count	Chapman (1939)
Fly	Farmland	Britain	Light trap	4	Count	Robertson (1939)
Fish	River	Mississippi, USA	Unknown	5	Count	Magurran (1988)

[a] C, Number of communities

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