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A Comparative Analysis of Evenness Index Sensitivity

key words: community structure, evenness measure, diversity, sensitivity analysis

Abstract

Evenness indices are numerous but the lack of knowledge of their properties is a limitation to their biological usefulness. 15 evenness indices, two of them being recently proposed, were studied in this work. We investigated the sensitivity of each index using (1) 189 macroinvertebrate communities sampled in the field, and (2) a set of communities modified in a controlled way.

There is no single way to measure evenness. We demonstrated that a measure should be chosen considering (1) the kind of data analysed and, (2) the index properties wanted by users. Depending on the ecological data set the index should be more sensitive to variations in rare, median or abundant species. For most of macroinvertebrate community analyses, a convenient evenness index requirs to be symmetric, unsensitive to variation on rare taxa, with a large range of variation and can be compared with a diversity index. Depending on diversity measure used, five indices correspond to these criteria: E_{Pielou}, $E_{Hurlbert}$, $E_{-ln(D)}$, E_{1-D}, E_{MI}. Our results were summarized in a table which may help users to select a convenient evenness measure according to their specific data. Concerning index properties, three main features that an evenness index should meet are briefly discussed: dependence with richness, symmetry criteria and variation range. A revue of this controversial subject allowed a best understanding of values obtained with evenness measures depending on their own features.

1. Introduction

No single diversity index is completely effective in describing community structure over a large range of situations. However, indices may be used under numerous conditions and can facilitate the ecological interpretation of vast data sets. They can be considered as a useful way to condense data and people with little biological expertise can (or should) easily understand them (NORRIS, 1995). In a survey of freshwater lotic and lentic studies, RESH and MCELRAVY (1993) showed that about 40% of studies used such indices.

Schematically, the diversity of a community is a function of both the number of taxa and the evenness with which the individuals are distributed among these taxa (PEET, 1974; MAGURRAN, 1988). Numerous mathematical functions have been proposed for measuring diversity and may be classified into families according to the main structural characteristic of a community that these functions measure namely, richness or evenness. These index families are more complementary than opposite. Many authors have recommended a simultaneous utilization of a set of indices, each of them belonging to one of these families (HAEDRICK, 1975; BOURNAUD and KECK, 1980; BOYLE *et al.*, 1990), because the use of a single index often leads to erroneous conclusions. Among these family indices, evenness measures give way to a specific interpretation of community organization.

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Different evenness indices can be recommended depending on the structural aspects of a community that users wish to measure (see SMITH and WILSON, 1996). For biological monitoring indices require more testing to evaluate (1) index variation range on a large set of communities sampled in the field, and (2) index sensitivity in order to determine if the degree of each evenness index response depends on the manner in which the community changed.

In this work, 189 freshwater macroinvertebrate communities were used. A simulation procedure allowed us to determine each index response when changes affect only a known part of a community (i.e., abundances of rare, median or dominant taxa). Even though we analysed simulations on freshwater invertebrate assemblages only, conclusions can be easily transposed to other communities.

Hence we investigated the properties of fifteen evenness indices and tried to answer to three fundamental questions for practical use of such indices in biological monitoring:

(1) Do all evenness indices measure the same community characteristic?

(2) What is the range in which each evenness index varies, when calculated on a large set of communities with very different structures?

(3) Does the magnitude of the index response depend on the community change modalities?

The discussion deals with properties needed for an evenness measure and their consequences on the specific choice of an index.

2. Materials and Methods

2.1. The Field Community Sampling Program

Field work was conducted in twelve localities in June and September of 1993. All study sites were located on 1st to 4th order streams situated in the north-eastern part of France. The range of physical variables, that were recorded on the sampling dates were: mean width, 2.5–11 m; mean depth, 12–35 cm; mean annual discharge, 0.5–5 m^3/s. Study sites slopes ranged from 0.05 to 1.5%, pH from 6.5 to 8.2, conductivity from 48 to 1080 µS/cm, and dissolved oxygen from 60 to 100%.

On each sampling occasion, eight to twelve substrate samples of 0.05 m^2, were collected within each study site. Benthic invertebrates were collected using a modified Surber sampler (mesh size 500 µm). The substrate within the sampler was removed to a depth of about 6 cm. Collected substratum was thoroughly brushed and washed to remove any additional organisms. All samples were preserved in 4% formaldehyde.

These samples described 189 benthic macroinvertebrate communities, and all index calculations were carried out on faunal lists at family level (with the exception of Oligochaeta and Hydracarina, which were recorded as such).

2.2. Tested Indices

Fifteen evenness indices (n° 5 to 19 in Table 1) were calculated on 189 communities. Fourteen of these indices were described and compared in terms of mathematical features by SMITH and WILSON (1996). The fifteenth, HURLBERT's index (HURLBERT, 1971), is derived from PIELOU's formula. It takes into account both the minimum and the maximum SHANNON diversity values. As a result, $E_{Hurlbert}$ ranges from 0 to 1 whereas E_{Pielou} ranges from the ratio [minimum diversity/SHANNON diversity] to 1. Many authors have considered minimum SHANNON diversity as being equal to zero probably to avoid the difficulty of calculating this limit. Therefore, the evenness measure systematically used has been E_{Pielou}. We proposed a very simple formula for calculating this limit when the data are in the form of counts (BEISEL and MORETEAU, 1997). All evenness index formulae were presented in Table 1 together with diversity and dominance indices needed for their calculation. All calculations were performed using natural logarithms.

Table 1. Usual names, formulae, references and codes of studied indices. S = number of taxa in the community, q_i = abundance of the i^{th} taxa, Q = total number of individuals in the community. Indices 1 to 4 are used for the calculation of evenness measures. *arctan* and *arcsin* are assumed to provide an angle in radians. Further details can be found in SMITH and WILSON (1996) or original references. Codes are in accordance with SMITH and WILSON (1996).

N°	Usual name	Formulae	Reference	Code
1	SHANNON-WEAVER Diversity	$-\sum_{i=1}^{S}(q_i/Q)\ln(q_i/Q)$	SHANNON and WEAVER (1963)	H'
2	SHANNON-WEAVER minimal diversity	$\ln(Q)-[(Q-S+1)\ln(Q-S+1)/Q]$	SHANNON and WEAVER (1963) modified	H'_{min}
3	SHANNON-WEAVER maximal diversity	$\ln(S)$	SHANNON and WEAVER (1963)	H'_{max}
4	Dominance index	$\frac{\sum_{i=1}^{s} q_i(q_i-1)}{Q(Q-1)}$	SIMPSON (1949)	D
5	PIELOU's evenness	H'/H'_{max}	PIELOU (1966)	E_{Pielou}
6	HURLBERT's evenness	$\frac{H'-H'_{min}}{H'_{max}-H'_{min}}$	HURLBERT (1971)	$E_{Hurlbert}$
7	MCINTOSH's evenness	$\frac{Q-\sqrt{\sum_i (q_i)^2}}{Q-Q/\sqrt{S}}$	MCINTOSH (1967)	E_{MI}
8	HEIP's evenness	$(e^{H'}-1)/(S-1)$	HEIP (1974)	E_{Heip}
9		$(1-D)/(1-1/S)$	SMITH and WILSON (1996)	E_{1-D}
10		$(1/D)/S$	SMITH and WILSON (1996)	$E_{1/D}$
11		$\frac{-\ln(D)}{\ln(S)}$	SMITH and WILSON (1996)	$E_{-\ln(D)}$
12	HILL modified evenness	$\frac{1/D-1}{e^{H'}-1}$	ALATALO (1981)	$F_{2,1}$
13		if $F_{2,1} > 0.5$ then $F_{2,1} 0.636611 \arcsin F_{2,1}$ else $F^3_{2,1}$	MOLINARI (1989)	$G_{2,1}$
14		$\sum_{i=1}^{S}\text{minimum}(q_i/Q, 1/S)$	BULLA (1994)	O
15	BULLA's evenness	$\frac{O-1/S}{1-1/S}$	BULLA (1994)	E

Table 1 (Continued)

N °	Usual name	Formulae	Reference	Code
16	CAMARGO's evenness	$1-\sum_{S1=1}^{S}\sum_{S2=S1+1}^{S}\lvert p_{S1}-p_{S2}\rvert / S$	CAMARGO (1992)	E′
17	SMITH and WILSON evenness A	$1-2/\pi\cdot\arctan\left\{\sum_{S=1}^{S}\left(\ln(x_s)-\sum_{t=1}^{S}\ln(x_t)/S\right)^2/S\right\}$	SMITH and WILSON (1996)	E_{var}
18	NEE's index	Slope of log abundance on the rank of abundance, fitted by least-squares regression	SMITH and WILSON (1996)	NHC
19	SMITH and WILSON evenness B	$-2/\pi\cdot\arctan(b')$ with b' = the slope of the scaled rank of abundance on log abundance, fitted by least-squares regression	SMITH and WILSON (1996)	E_Q

The simulation procedure exposed here completes some theoretical works that follow a mathematical approach for analysing bias and variances of some diversity indices.

2.3. Simulation Procedure

A series of simulations was performed to evaluate the relative sensitivity of the fifteen evenness indices. The main goal of these simulations was to mathematically generate variations in communities that could be expected to be found in collections gathered by biologists in different ecosystems. For example, in the specific case of aquatic macroinvertebrates, there are many natural or technical sources of quantitative variations in faunal structure of samples, for example: (1) spatial variations in the microdistribution of stream invertebrates (DOWNES *et al.*, 1993); or (2) variations in abundance estimates related to subsampling (ROSILLON, 1984), differences in sampling equipment (MACAN, 1958; ROSILLON, 1984) and/or variability in operator efficiency (CLIFFORD and CASEY, 1992).

Each sample was considered as a representative picture of the invertebrate community of a habitat. Each community was altered in three ways.

– Type I simulations were designed to modify as much as possible the number and the abundance of rare taxa. Rare taxa were defined as taxa with a number of individuals < 4 and a relative abundance < 5%. Faunal lists were modified firstly by taking out rare taxa, and secondly by adding a random number of chosen taxa, between 0 and 2n, to the truncated faunal list (if n is the number of rare taxa). Each of the potentially new rare taxa also had a random abundance of 1, 2 or 3 individuals.
– For type II simulations, abundances of the median taxa (i.e., those that exhibited a relative abundance between 5 and 40%) were individually multiplied by a given factor randomly chosen between 0.75 and 1.25.
– Type III simulations changed the community in such a way that the abundance of the most common taxa (i.e., those which had a relative abundance greater or equal to 40%) was multiplied by a given factor chosen randomly between 0.75 and 1.25.

Conducting 100 simulations of each type on the 189 sampled communities would add up to $100\times 3\times 189 = 56{,}700$ faunal lists, and (× 15 indices) 850,500 values of evenness indices. To simplify, we attempted to reduce the number of faunal lists without excluding some community structure 'types'. A standardized principal components analysis was performed on a set of 19 indices (abundance, richness, diversity and dominance indices) in order to clearly bring out information on the community structure organization of our 189 samples (for details, see BEISEL, 1996). Then, a cluster analysis with

WARD's method was conducted on the 189 sample factorial scores of the first five PCA axes (representing 92% of explained variance). Samples were subdivided into 20 groups according to their faunal structure. Each of these groups was characterized by two samples located close to the centre of their group. One group was only composed of a single sample; therefore, the total number of selected faunal lists was 39. All simulations were then performed on the faunal list of these 39 representative samples.

For each simulation type (I, II or III), a set of 3,900 simulated lists was created (i.e., 39 selected samples × 100 simulations). Evenness indices were calculated to characterize each community structure. For a given index the variation, in evenness estimates among simulated lists of a community, was evaluated by means of a coefficient of variation (CV). CV is the standard deviation expressed as a percentage of the mean. This measure allowed us to obtain a comparable description of the relative amount of variation for indices with different means and/or different units of measure. For each sampled community, CV was calculated on 100 simulated lists.

Our 39 selected faunal lists represented a set of varied community structure. For example, richness ranged from 4 to 33 taxa, and the SHANNON-WEAVER diversity index varied from 0.08 to 2.60. All lists did not simultaneously exhibit rare, median and abundant species as defined above. Only thirty eight lists displayed rare taxa, thirty five had median taxa, and twenty seven had dominant taxa. Finally, we obtained an [15 indices × 38 CV] array for simulations of type I, an [15 indices × 35 CV] array for simulations of type II, and an [15 indices × 27 CV] array for simulations of type III. Box-whiskers graphs depicted the order of magnitude and the variability of CV for each index and each simulation type.

2.4. Statistics Used

There was no reason to assume that a relationship between two indices would be linear. Furthermore, several indices did not follow the principle that their observed values were drawn from normally distributed populations. For both of these reasons, we chose a nonparametric procedure in correlation analysis. The SPEARMAN rank correlation coefficient (r_S) enabled us to define relationships between pairs of evenness indices.

The Euclidean distance and WARD's method were used in cluster analysis in order to objectively identify groups of indices exhibiting the same sensitivity spectrum. The Euclidean distance increases with the difference between two evenness indices. This metric all the more magnifies the difference of result between two indices as their variation ranges differe. The clustering algorithm used is designed for the constitution of homogeneous groups of evenness measures. WARD's method is a good compromise between divisive and agglomerative methods and is compatible with an Euclidean metric.

3. Results

3.1. Sensitivity of Evenness Indices on a Set of 189 Communities

All indices, excepted NHC, range in an interval from 0 to 1 (Fig. 1, NHC is not shown). Median values ranged between 0.75 and 0.07 (0.22 if we excluded E_Q), and were very variable among tested indices. Consequently, indices were not similar in terms of evenness value distribution for a set of 189 communities.

We can notice that E_Q differed from all the other evenness measures. It only ranged between 0.05 and 0.24, a narrow interval of variation for an index which can mathematically range from 0 to 1. This evenness measure did not allow us to detect significant differences in evenness among 189 communities while all the other indices made it potentially possible.

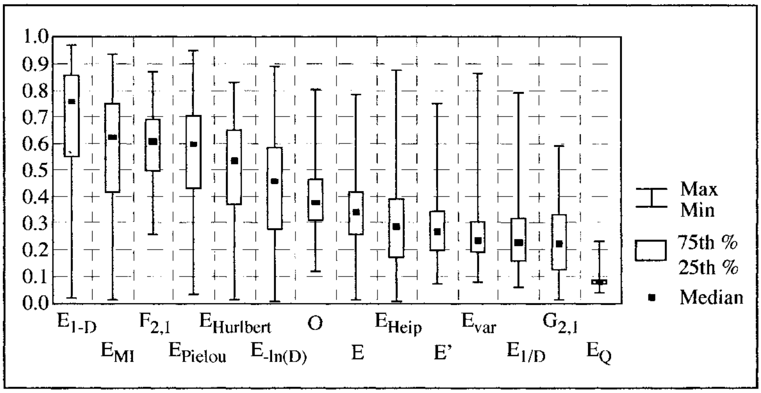

Figure 1. Variation ranges of fourteen evenness measures calculated on a set of 189 communities. See Table 1 for codes of evenness measures.

3.2. Between-Indices Relationships

Most of SPEARMAN correlation coefficients were highly significant ($p < 0.01$, Table 2). Twenty-nine of them were superior or equal to 0.90. Some of the lower (but significant) correlations concerned E_{var} and E_Q. They illustrated the difference of results between these two measures and all other evenness indices.

On the contrary, three correlations were not significant ($p > 0.05$) and one was significant but at a lower level ($0.05 < p < 0.01$). All of them concerned NHC, which do not seem to measure the same characteristic of a community as other evenness indices. This illustrates the differences among concepts in which evenness indices are based.

The cluster analysis allowed us to split indices into different groups, which corresponded to different concepts (Fig. 2). Calculations were performed on standardized variables. We

Table 2. SPEARMAN's correlation coefficients calculated between evenness measures ($n = 189$). All correlations are significant with $p < 0.01$, excepted for the underlined values ($0.05 < p < 0.01$), and for the values in italics ($p > 0.05$). Codes are in Table 1.

	E_{Pielou}	$E_{Hurlbert}$	E_{Heip}	E_{1-D}	$E_{1/D}$	$E_{-ln(D)}$	$F_{2,1}$	$G_{2,1}$	O	E	E_{MI}	E′	E_{var}	E_Q
$E_{Hurlbert}$	0.94													
E_{Heip}	0.97	0.89												
E_{1-D}	0.96	0.97	0.88											
$E_{1/D}$	0.85	0.76	0.94	0.76										
$E_{-ln(D)}$	0.98	0.95	0.95	0.97	0.87									
$F_{2,1}$	0.68	0.69	0.71	0.72	0.81	0.79								
$G_{2,1}$	0.68	0.69	0.71	0.72	0.81	0.79	1.00							
O	0.93	0.84	0.97	0.80	0.90	0.89	0.60	0.60						
E	0.97	0.91	0.96	0.89	0.83	0.93	0.59	0.59	0.97					
E_{MI}	0.97	0.97	0.92	0.99	0.81	0.99	0.76	0.76	0.84	0.91				
E′	0.89	0.78	0.97	0.77	0.96	0.87	0.66	0.66	0.97	0.90	0.81			
E_{var}	0.69	0.51	0.72	0.53	0.59	0.59	0.19	0.19	0.74	0.73	0.56	0.75		
E_Q	0.77	0.62	0.79	0.62	0.65	0.67	0.26	0.26	0.81	0.81	0.65	0.81	0.97	
NHC	0.46	0.48	0.29	0.56	*0.02*	0.41	*–0.03*	*–0.03*	0.26	0.42	0.50	<u>0.16</u>	0.43	0.44

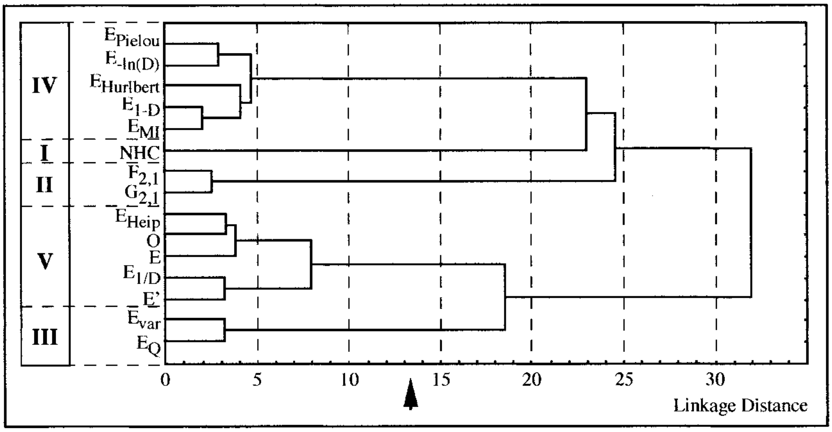

Figure 2. Cluster analysis on fifteen evenness measures calculated on a set of 189 communities. Values were standardized [standardized value = (initial value – mean of evenness measure) / standard deviation of evenness measure] in order to compare evenness measures with the same range of variation. Euclidean distance and WARD's method of linkage were used in the tree clustering method. An arrow indicates the level of truncation. Five groups of indices (I, II, III, IV and V) were constituted (see text for further details).

chose to truncate the dendrogram at a high level of distance in order to reduce the probability of separating measures which in fact could have given quite similar results.

Five groups were formed. The first group was solely composed of NHC. This index appeared to be very different from all the others although values were standardized. A second group was composed of $F_{2,1}$ and $G_{2,1}$. These two indices were the only two which did not decrease when the abundance of the most minor species in a community was marginally reduced (SMITH and WILSON, 1996). Consequently, they can give very different results compared to all other indices. Some of the non-significant correlations concerned these two indices. A third group was composed of E_{var} and E_Q. E_{var}, E_Q and NHC are the only three indices which are symmetric with regard to minor and abundant species (SMITH and WILSON, 1996). The composition of the two last groups was more difficult to explain. A fourth group consisted of E_{Pielou}, $E_{Hurlbert}$, $E_{-\ln(D)}$, E_{1-D}, and E_{MI}. The last group included all the other indices: i.e., E_{Heip}, O, E, $E_{1/D}$, and E'. One hypothesis was that group 4 corresponded to measures less sensitive to variations in rare species richness and/or abundances than measures of the group 5.

3.3. Sensitivity of Evenness Indices on a Set of Simulated Lists

For one type of simulation, evenness indices were compared according to their CV for thirty nine sets of one hundred simulated lists (see above). A CV is particularly high when an index gives variable results for a set of simulated lists (Fig. 3). The box-whiskers graph takes into account the range of variability of the CV for the 39 sets of simulated lists. A cluster analysis enabled us to identify groups of evenness indices which had the same range of variability for each set of simulations.

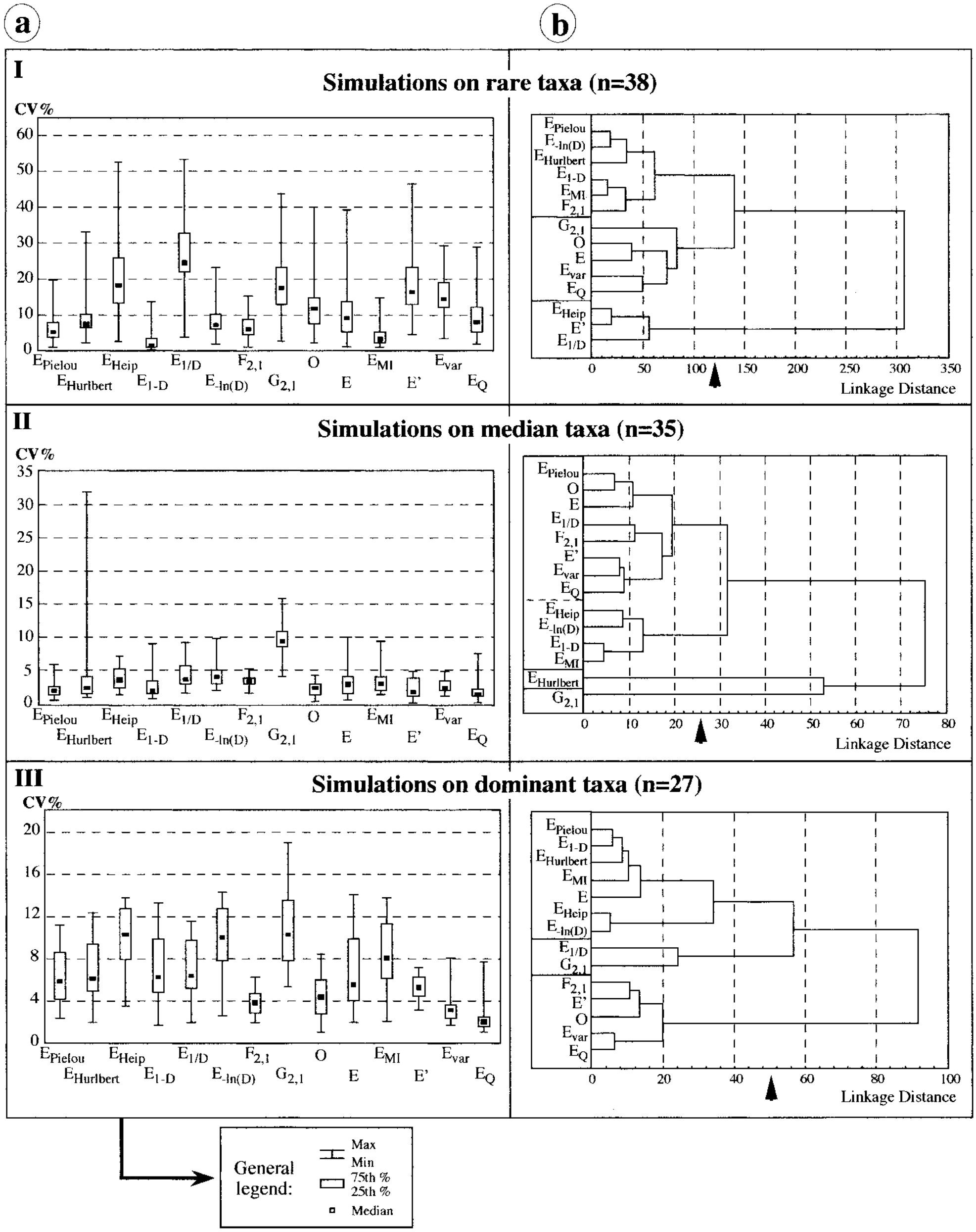

Figure 3. a – Variability of the coefficients of variation (CV) calculated on thirty nine communities, for fourteen evenness indices. For each index and each community, a set of a hundred simulations generated a hundred evenness values. Three types of simulations were performed [type I = on rare taxa; type II = on median taxa; type III = on dominant taxa – see text for further details]. Each value distribution was summarized by its coefficient of variation. Box-whiskers graphs illustrated the distribution of a set of thirty nine CV, for each evenness index.

b – Ordination of indices by cluster analysis. Euclidean distance and WARD's method of linkage were used in the tree clustering method. Codes are in Table 1. An arrow indicates the level of truncation.

3.3.1. Variations on Abundances of Rare Taxa

On the basis of the cluster analysis, three groups of indices may be constituted depending on the variability of indices to minute changes in richness and abundance of rare taxa of tested communities.

The first group (i.e., E_{Pielou}, $E_{Hurlbert}$, E_{1-D}, E_{-lnD}, $F_{2/1}$, E_{MI}) was constituted with indices which were the least sensitive indices to variations on rare taxa. Even if their CV could be relatively high for simulations of a given list (see for example the range of variation of $E_{Hurlbert}$), the average CV of these indices were always low. The second group (i.e., $G_{2,1}$, O, E, E_{var}, E_Q) was composed of measures which had an intermediate sensitivity to variations on rare taxa. The third group included E_{Heip}, $E_{1/D}$ and E′, which exhibited the higher mean CV for this type of simulation. However, differences between the second and the third group were not only based on the mean CV. We noted that both $G_{2,1}$ and E′ had approximately the same CV average and the same range of CV. Yet, they were not in the same group. The cluster analysis illustrated the different intensity of response of these two indices to the same changes in a community.

3.3.2. Variations on Abundances of Median Taxa

The analysis of results obtained with variations on abundances of median taxa was more complex. Three groups could be observed. The first group was only constituted with $E_{Hurlbert}$. This result was in fact the consequence of one exceptional value of CV which was very important with regard to other CV values. However, it is interesting to know that in some cases of community structure $E_{Hurlbert}$ could strongly fluctuate with minute variations of the faunal list. Yet, if we excepted this value the box-whiskers graph changed only slightly.

The cluster analysis also demonstrated that the $G_{2,1}$ index was very different from all other indices and had to constitute a second group. It seemed to have the highest level of sensitivity to variations on median taxon abundances. Its average CV was at least two times higher than average CV of other measures.

Except for $G_{2,1}$, the range of variation of the evenness index CV was small. Consequently, all other indices may be considered as being in a third group. The cluster analysis in fact allowed us to subdivide this group into two subgroups. The first subgroup was constituted with E_{Heip}, E_{-lnD}, E_{1-D} and E_{MI}. Among measures exhibiting a low sensitivity to variations on median taxon abundances, they could perhaps be considered as the most sensitive evenness indices. The second subgroup included E_{Pielou}, O, E, $E_{1/D}$, $F_{2,1}$, E′, E_{var} and E_Q.

3.3.3. Variations on Abundances of Dominant Taxa

Three groups of evenness measures may be distinguished according to their sensitivity to variations on dominant taxon abundances. The first group included $E_{1/D}$ and $G_{2,1}$. $G_{2,1}$ exhibited the higher sensitivity. $E_{1/D}$ exhibited a sensitivity similar to indices which belong to the second group (see the box-whiskers graph on fig. 3), but the cluster analysis emphasized (1) some specific response to given variations on abundances of dominant taxa (but not observed when the total response distribution is considered), and (2) some connection between $E_{1/D}$ and $G_{2,1}$ responses to the same changes in abundances. E_{Pielou}, $E_{Hurlbert}$, E_{1-D}, E, E_{MI}, E_{Heip}, E_{-lnD} were indices with a median sensitivity and formed a second group. In this group, E_{Heip} and E_{-lnD} were the most sensitive indices to variations on abundances of dominant taxa. The third group, well differentiated, was composed of the least sensitive measures to variations on dominant taxa: $F_{2,1}$, O, E′, E_{var}, E_Q.

4. Discussion

Although evenness is a long studied concept, there is no consensus on how a measure of evenness should be chosen. In our opinion, following ALATALO (1981) and SMITH and WILSON (1996), there is no single way to measure evenness. In practice, choice of an evenness index should depend on two interdependent parameters: (1) the kind of data studied and, (2) the index properties wanted by users.

4.1. Importance of the Kind of Data

The kind of data studied has a strong influence on the choice of an evenness measure. Two main ideas have to be considered.

All evenness measures do not display the same sensitivity to abundance variations of rare, median or abundant taxa. We argue that it is a required quality in the sense that the degree of response of an evenness index has to depend on the manner in which a community structure is modified. Two reasons may be evoked: (1) a particular sensitivity to a type of taxon abundance variations may be sometimes interesting; (2) according to the sampling procedure, a variable level of precision can exist on the estimation of abundances of rare, median or abundant taxa. Indeed, users often desire a particular sensitivity to rare, median or abundant species, depending on the community structure which can be very different from one biotope to another. For example, phytosociologists who analysed changes in a grassland, are particularly interested in indicator species which are often rare species (i.e. plant species feebly represented). To emphasize spatial or temporal differences, they have to choose an index with a high sensitivity to rare species. In contrast, limnologists studying the variability of zooplankton community structure induced by environmental changes are perhaps more interested in measures with a high sensitivity to changes in abundances of dominant taxa. Consequently, depending on the ecological framework, it may be interesting to evaluate the proportion of rare, median and dominant taxa in the community [with a rank-abundance diagram or a relative abundance distribution model as suggested by FRONTIER and PICHOD-VIALE (1993), MOUILLOT *et al.* (2000)], and to use an index more or less sensitive to changes in abundances of one of these categories of taxa.

Furthermore, there is always some uncertainty on the estimation of species abundances due both to the sampling design and to the field work protocol. This degree of uncertainty on community structure can highly influence the choice of an evenness index. For example, in the specific case of freshwater ecosystems, most benthic macroinvertebrate species exhibit aggregate distributions. Consequently, rare species are especially difficult to be efficiently sampled. Their abundance estimations are subject to a relative interval of uncertainty greater than for other taxa. Under these conditions, a good evenness measure should preferably exhibit a weak sensitivity to variations on rare taxon abundances ($E_{Hurlbert}$ for example).

In addition, the sensitivity of some evenness indices depends on the diversity range of communities. For example, the relationship between HEIP's evenness and SHANNON's diversity may be described as a positive exponential curve (see formulae in Table 1). Consequently, sensitivity to variations in evenness is lower for communities with low diversity than for communities with high diversity. In contrast, if a searcher only works on communities with high diversity (for example plant communities in tropical forests), he might be interested in the higher sensitivity of HEIP's evenness in the high diversity range. In such a case, this index will help to detect minute changes in community structure in terms of distribution of individuals into taxa. Such relationships between evenness and diversity measures have to be inferred from the evenness formulae. They exceed the purpose of this paper but more information could be found in MAGURRAN (1988), and LUDWIG and REYNOLDS (1988).

4.2. *Choice of an Evenness Index Depending on its Properties*

The properties that an evenness index should meet constitute a controversial subject that has been recently studied in details by SMITH and WILSON (1996). Briefly, to complete our results, three main criteria need to be discussed.

The first requirement for an evenness measure is to be independent of species richness because in such a case evenness is supposed to be easier to interpret (SMITH and WILSON, 1996). We agree with this point of view which is idealistic but a weak relationship between a community richness and an evenness measure is not really a problem for the interpretation of community structure, mainly because richness is known, and it is easier to interpret two dependent variables we are capable of evaluating. Consequently, it is to be hoped that richness and evenness are independent, but it is not essential that this independence is complete.

A second important criterion is the symmetry of the response with regard to minor and dominant species abundances. On this controversial question, we do not think that, in practice, this criterion is desired. The choice of an index which includes this quality depends on the biological sense given to evenness. In ecology, it is generally understood that evenness quantifies the homogeneity of species abundances, even if a community with similar abundances for all these populations is unrealistic. For example, let A and B be two communities with 4 species. Species abundances are 400, 400, 400, 1, (33.3%, 33.3%, 33.3%, 0.1%) in community A and 1, 1, 1, 400 (0.3%, 0.3%, 0.3%, 99.1%) in community B. According to the symmetry criterion, these two communities should have the same evenness. But ecologically, it must be assumed that community A is more homogeneous because its distribution of species relative abundances is more even (variance of relative abundances is lower for A than for B). Consequently, similar changes in abundances (e.g. low variations of individuals) should have a lesser impact on the evenness of community A than on community B. E_{var} and E_Q are the only two indices which do not differentiate the structure of both communities.

In a second example, let C and D be two communities with respectively four and five species. Species abundances are 800, 800, 800, 800 in community C, and 800, 800, 800, 800, 1 in community D. The fifth species with a single individual represents the only difference between the two communities. For C, $E_{var} = 1$ and $E_Q = 1$ and for D, $E_{var} = 0.05$ and $E_Q = 0.09$. For a biologist, in most cases, such large differences in values do not correctly quantify the difference of evenness *sensu stricto* between both communities (according to the potential range of variation of these indices). This example gives another illustration of the ambiguity of the symmetry property for an evenness index. In the specific case of benthic invertebrate communities, accidental species (as for example resulting from drift in running waters) are not interesting for the community structure analysis even if their presence can not be blinded. Consequently, using a symmetric index may give an excessive weight to such species in the interpretation of community structure.

A third criterion is the variation range of an index for calculations realized on a given set of data. If an index is only slightly affected by considerable changes in community structure, it must be avoided. Our study showed that for one set of 189 communities E_Q exhibited only minute variations (Fig. 1) and consequently, the use of this index may lead users to erroneous conclusions. All other tested indices do not have this defect.

In conclusion, our results showed that all evenness indices do not measure the same community characteristics, the most different from the others being NHC.

It clearly appeared that the magnitude of evenness index response depended on the community change modalities. Our analysis of the different degree of sensitivity of 15 evenness indices to rare, median or dominant species can help users to chose an index according to features of their ecological data. Our results summarized in Table 3 should allow to select an index in this way. It may be noticed that if data are in the form of counts, the use of

Table 3. Summary of the results of testing evenness indices on simulated communities. The sensitivity concerns evenness response to density variations of rare, median or dominant taxa. Key: + = strong sensitivity, – = weak sensitivity, ns = not studied. Special feature(s) of an index can be read in the column 'Observation'.

	SENSITIVITY Rare	Median	Dominant	Observation
E_{Pielou}	–			
E_{1-D}	–			
E_{MI}	–			
$E_{-\ln(D)}$	–			
$E_{Hurlbert}$	–	can be strong		
$F_{2,1}$	–		–	• does not decrease when most minor species decrease
$G_{2,1}$		+	+	• does not decrease when most minor species decrease
E				
O			–	• does not range between 0 and 1
E_{var}			–	• symmetric measure
E_Q			–	• symmetric measure • weak range of variation
E_{Heip}	+			
$E_{1/D}$	+			
E′	+		–	
NHC	ns	ns	ns	• does not range between 0 and 1

$E_{Hurlbert}$ (HURLBERT, 1971) is better than the use of E_{Pielou}, because $E_{Hurlbert}$ really ranges from 0 to 1 (BEISEL and MORETEAU, 1997).

Our results complete requirements of evenness index describe in theoretical comparative works. If we accept that symmetry is not a desirable feature for evenness index, the analysis of community structure may be completed by the calculation of a dominance index which allows evaluating if only one or a few taxa are very abundant in a community. Recent studies can help users in the choice of a dominance index (MAGURRAN, 1988; BEISEL *et al.*, 1996).

In addition, any evenness index should not be used alone. Because diversity integrates in a dual scheme richness and evenness, we think that the utilization of richness, evenness and diversity indices cannot be separated. Evenness indices can be considered as relative diversity indices (PEET, 1974) or normalizations of diversity indices (KVALSETH, 1991). Consequently, we think that any evenness measure must be interpreted with both the richness and the diversity indices integrated in its calculation. This strategy could perhaps facilitate the data interpretation, and decrease the importance of the wanted independence between an evenness index and richness.

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