



## Sensitivity of diversity indices: a study of dipterous assemblages

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**Abstract:** It is an essential property of diversity indices that increases in the abundance or frequency of the most frequent species result in a decline in diversity, whereas increases in the abundance of the rarest species lead to an increase in diversity. At the same time, without resort to mathematical operations, it is difficult to determine the sign and measure of alteration in diversity when increasing an additional frequency while leaving all others unaltered. A more concrete task is to determine the index response to a partial alteration of fixed percentage in the frequencies of the multi-species community or collection. Plotting the observed responses or sensitivity values against the frequencies concerned makes possible a good overview of the sensitivity relations. The mathematical groundwork of sensitivity analysis with respect to diversity indices has already been elaborated. To date, however, the methodological possibilities engendered by such analyses have yet to be exploited.

In the present work, sensitivity relations are discussed for apple-bait Drosophilidae collections and human faeces trap collections of flies inhabiting brook valleys in the low mountains of Hungary. Inspection of the results enables us to identify the range of frequencies at which significant increases or decreases in diversity will result. A relatively small increase of so-called nearly indifferent or quasineutral frequencies lying within that frequency range has a trivial influence on diversity values. While sensitivity is astonishingly sizeable with a few dominant case numbers, all other frequencies scarcely influence the index value.

### Introduction

It is an essential property of diversity indices that increases in the abundance or frequency of the most frequent species result in a decline in diversity, whereas increases in the abundance of the rarest species lead to an increase in diversity. At the same time, without resort to mathematical operations, it is difficult to determine the sign and measure of alteration in diversity when increasing an additional frequency while leaving all others unaltered. Data on diversity index sensitivity are well represented in the literature beginning in the 1970s (Peet 1974, Smith and Grassle 1977, Kempton and Wedderburn 1978, Magurran 1988, chap. 4). Some years later numerical experiments were carried out by Boyle (1990). The general mathematical background and certain other aspects of sensitivity analyses have been touched upon by Taillie and Patil (1979) and by Patil and Taillie (1982). Schmid (1991) has developed a sensitivity concept closely related to the transfer principle for inequality measures used mainly in economics. It is well-known that counterparts of these measures can be regarded as evenness measures.

Following these methodological explorations, an adequate mathematical background to sensitivity analysis was worked out by Izsák (1991, 1992, 1996). Subsequently, the authors of the present article briefly discussed an ecological case study in a paper on several methodological possibilities of diversity investigations (Izsák and Papp 1994) and developed a computer program for sensitivity calculations (Izsák 1998). In the present article we discuss in more detail the possibilities of sensitivity analysis of diversity indices, while also focussing on several practical aspects. For example, we introduce a simple sensitivity parameter which provides a joint characterisation of various sensitivity properties of diversity indices. We also touch upon the ecological applicability and feasibility of index sensitivity studies. Our aim is to call the attention of ecologists to the usefulness of additional data on diversity relations which can be obtained with a minimum of extra effort.

The outlined sensitivity analysis facilitates development of a more flexible means of representation with re-

spect to the relations between diversity and changes in the community structure.

## Materials and methods

As test samples we chose the species frequencies in dipterous assemblages of brook valleys in the low mountains of Hungary. Simultaneously and at the same 4 sites, collections of both Drosophilidae and synanthropic flies were obtained with the aid of apple-bait and Gregor-Povolny traps baited with human faeces, respectively, in 1988-1990. The collections numbered 8895 drosophilid specimens of 40 species and 9191 synanthropic fly specimens of approximately 200 species. Descriptions of the sites and collection methods can be found in Papp (1992, 1993a). In the present study, we analyse the frequencies at the Aggtelek site (valley of the Ménes Brook, 150 metres downstream from its source, in Aggtelek National Park, Aggtelek, Hungary), where 10 Drosophilidae samples yielded 1691 specimens of 31 species (Papp 1992, Izsák and Papp 1994) and 9 synanthropic samples 3701 specimens of 10 species (Papp 1993a). Although the sample sizes are seemingly large, the large number of singletons (56 singletons among the synanthropic flies) indicates the high sample variability.

### Sensitivity calculations

The mathematical background to the sensitivity analysis has been described elsewhere (Izsák 1991, 1992, Izsák and Papp 1994).

Denote with  $D$  the diversity function. The linear approximation of the change in the index value  $D(n_1/n, n_2/n, \dots, n_s/n)$ , obtained by increasing the frequency  $n_k$  to  $n_k + tn_k$  and fixing the other frequencies, is:

$$\delta_{n_k} = (\partial / \partial x_k) D(x_1/x, x_2/x, \dots, x_s/x) \cdot t \cdot n_k \quad (k = 1, 2, \dots, s).$$

Here  $n = \sum n_i$ ,  $x = \sum x_i$  and  $\mathbf{x} = (x_1, x_2, \dots, x_s)$  is the continuous form of the  $\mathbf{n} = (n_1, n_2, \dots, n_s)$  frequency vector. We believe that analysing the effects of fixed proportionate changes in the abundances is a more reasonable procedure than analysing the effects due to fixed absolute changes. According to the above formula, characterisation of the sensitivity relating to the same proportionate partial increase in the frequencies can be obtained with the quantities:

$$\Delta_{n_k} = \delta_{n_k}/t = (\partial / \partial x_k) D(x_1/x, x_2/x, \dots, x_s/x)|_{\mathbf{x}=\mathbf{n}} \cdot n_k \quad (k = 1, 2, \dots, s).$$

To clarify the meaning of  $\delta_{n_k}$  and  $\Delta_{n_k}$ , take the Shannon index  $H$ . The concrete form of  $\delta_{n_k}$  is now:

$$\begin{aligned} \delta_{n_k} &= \frac{\partial}{\partial x_k} \left( - \sum \frac{x_i}{x} \ln \frac{x_i}{x} \right)_{\mathbf{x}=\mathbf{n}} \cdot t \cdot n_k = \\ &= \left( - \frac{1}{\sum n_j} \ln \frac{n_k}{\sum n_j} + \frac{1}{(\sum n_j)^2} \sum n_i \ln \frac{n_i}{\sum n_j} \right) \cdot t \cdot n_k = t \cdot \Delta_{n_k} \end{aligned}$$

(Izsák 1992). For example, for the abundance vector of the sample from synanthropic flies (1442, 288, 218, ..., 1); see Table 1, where the sample size is 3701 and  $\Delta_{63} = \Delta_{n_8}$  equates to 0.0267. That is, by increasing the frequency 63 to  $63 + 0.10 \cdot 63 \approx 69$ , the linear approximation of the change in  $H$  is  $0.10 \cdot 0.0267 = 0.00267$ , which is a rather small value relative to the original value 2.5878. Similar small changes can be obtained for almost all other frequencies. All of these are positive, with the exception of 244 and 1442. The only essential change in  $H$  following a 10 percent change in the frequency belongs to 1442. This change of the index value is  $0.10 \cdot (-0.8721) = -0.08721$ .

Why not drop whole frequency when studying sensitivity relations, as it is reasonable to ask? Although, this is undoubtedly another possible approach to the problem, such a radical change in the species structure is mostly unnatural. Another direct numerical method of sensitivity analysis could involve partial increase of the frequencies, e.g., by five percent, and recalculation of the index value after each perturbation. The change in the index is the difference between the original and new index value. Switching over to another  $t$  percent increase of the frequencies, the change in the index value is approximately the former one multiplied by  $t/5$ . Unfortunately, ecologists do not employ even this rather simple sensitivity analysis! Naturally, the same can be done in the case of the more exact mathematical method. Continuing with the example, after the above calculations it is easy to give the change in  $H$  by changing the frequency 63 to  $63 - 0.05 \cdot 63 \approx 60$ . The result is a change of  $-0.05 \cdot 0.0267$ , that is a 0.00133 decrease (!) in  $H$ . In addition, our mathematical method and the formulae on sensitivity also make possible a formal mathematical analysis of sensitivity properties, which is impossible in the case of such numerical experiments.

Numerical calculations were performed using the appropriate routine in the DIVERSI 1.1 program package (Izsák 1998). We analysed the sensitivity of the following indices: Hurlbert indices  $E_m$  with  $m = 2$  and  $m = 50$ , Shannon index  $H$  and Hill index  $N_a$  with  $a = 0.5$ . Choice of these indices can be justified on the following grounds.

Index  $E_2$  is extremely sensitive to changes in small frequencies. A further motivation is that  $E_2$  equals to  $1 + GS$ , where  $GS = \sum_i (n_i / \Sigma n_i)^2$  is the widely used Gini-Simpson index. Thus, by analysing the sensitivity of  $E_2$ , we also analyse the sensitivity of the well-known Gini-Simpson index.  $H$  is the most frequently used diversity index. Similarly to  $E$ ,  $H$  also overemphasises the changes in the leading frequencies. Index  $E_{50}$ , another member of the  $E_m$  index family with a rather large  $m$  parameter, is less sensitive to changes in the largest frequencies than are  $E_m$  indices with a small  $m$  parameter. The literature (Hill 1973, Kempton 1979) and our own experience (Izsák and Juhász-Nagy 1984) suggest that this is also true of  $N_a$  indices with small  $a$  parameters. To sum up, we analysed the sensitivity of two indices ( $E_2$  and  $H$ ) with high sensitivity and two other ones ( $E_{50}$  and  $N_{0.5}$ ) with relatively low sensitivity to changes in the largest frequencies.

The concrete form of  $\Delta_{nk}$  for the Shannon index is given above. The formulae for the parametric indices  $E_m$  and  $N_a$  are the following.

Hurlbert index,  $E_m$  :

$$\Delta_{n_i} = \frac{\partial}{\partial x_k} E_m(\mathbf{x})|_{\mathbf{x}=\mathbf{n}} \cdot n_k = \frac{\partial}{\partial x_k} \sum \left( 1 - \left( 1 - \frac{x_i}{x} \right)^m \right) |_{\mathbf{x}=\mathbf{n}} \cdot n_k =$$

$$= \frac{m}{k} \left[ \left( 1 - \frac{x_k}{x} \right)^{m-1} - \sum \frac{x_k}{x} \left( 1 - \frac{x_k}{x} \right)^{m-1} \right] |_{\mathbf{x}=\mathbf{n}} \quad (m = 1, 2, \dots)$$

(Izsák 1991).

Hill index,  $N_a$  ( $a > 0$ ):

$$\Delta_{n_i} = \frac{a}{1-a} \left[ x^{\frac{a}{1-a}-1} x_k^{\frac{a}{1-a}-1} \left( \sum x_i^a \right)^{\frac{1}{1-a}} - x^{\frac{1}{1-a}-a} \left( \sum x_i^a \right)^{\frac{1}{1-a}} \right] |_{\mathbf{x}=\mathbf{n}} \cdot n_k$$

(Izsák and Papp 1994).

The computed sensitivities are given in Tables 1 and 2. For a good overview of the results, it is practical to construct so-called *sensitivity profiles*, obtained by plotting the sensitivities or index responses against the frequencies (Figs 2-3). Actually, for practical purposes, we plotted the relative sensitivities or index responses  $\Delta/\Delta_{max}$  against the logarithms of  $n_i$ , where  $\Delta_{max}$  is the maximum of the positive sensitivity values yielded. In this case, the maximal ordinate value is 1. Following standard practice, in the case of the rank – abundance curves (Fig. 1) we plotted all  $(r, \Delta_r)$  points even if  $\Delta_r = \Delta_{r+1} = \dots$ . The exception is fre-

quency 1; where we plotted a single point (*rank of 1; log 1*) = (*rank of 1; 0*).

We recall our remark on the sign of  $\Delta$ : if one were to investigate the index response to a *decrease* of the frequencies at a fixed proportion, the new sensitivity profile could be obtained by mirroring the original profile on the horizontal axis. The normalisation has no practical influence on the intersection of the profiles with the horizontal axis. Similarly, normalising does not influence the maximum site of the sensitivity profile. (We will take up this position parameter in the following section.) The index response relating to the largest frequency and possibly some following frequencies are negative numbers with extremely large absolute value. For practical purposes, we omitted the points concerned from the profiles. On the other hand, these sensitivity data, presented in Tables 1-2, are very informative.

## Results and discussion

To gain general information on the community structures, we fitted the truncated lognormal abundance model to both species abundance sets. The model fits both of them well. The chi-square value is 4.84 (df = 7) with the synanthropic flies and 8.03 (df = 7) with the drosophilid flies. The critical chi-square level with this degree of freedom is 14.07 for  $p = 0.05$  and 18.47 for  $p = 0.01$ . Further impressions of the community structure can be obtained by constructing rank – abundance curves. Actually, for practical purposes, we plotted the logarithms of the decreasingly ordered abundances against their rank.

As is well known, the rank – log(abundance) curve shows in the case of lognormally distributed abundances a characteristic, nearly linear section, known as an  $\alpha$  section. This stretches from about the 12<sup>th</sup> to the 26<sup>th</sup> species with the synanthropic flies collection and from about the 9<sup>th</sup> to the 16<sup>th</sup> species with the drosophilid flies collection (Fig. 1). It is suggested that the shaping of that section reflects congestion of two species groups. Some species, which possess the biological potentials to be abundant in favourable conditions, have a medium sized population under the existing conditions. Other species are truly rare, but their populations are much larger than usual, mostly due to chance (Papp 1993b). The good fit of the results and the observability of the  $\alpha$  section in the groups under study assure that the observed sensitivity relations are rather general.

As mentioned in the methodological section, we present the tables with the original sensitivity data and the sensitivity profiles (Figs. 2-3) as well. Tables 1-2 show that the sensitivities relating to some of the leading fre-

**Table 1.** Species abundances or frequencies and basic sensitivity data for synanthropic flies. \*: the value representing  $\Delta_{max}$ , +: the corresponding relative value is not shown in the profile.

sensitivity ( $\Delta_n$ )					
frequency ( $n$ ) (with multiplicities)	rank ( $r$ )	$E_2$	H	$E_{50}$	$N_{0.5}$
1442	1	-0.2202+	-0.8721+	-5.3115+	-17.7463+
244	2	0.0258*	-0.0052	-0.8319+	-1.8546+
218	3	0.0243	0.0035	-0.7091+	-1.5559+
120	4	0.0159	0.0254	-0.1673	-0.5034+
86	5	0.0120	0.02764	0.0301	-0.1831
85	6	0.0119	0.02765*	0.0355	-0.1743
70	7	0.0100	0.0272	0.1099	-0.0468
63	8	0.0091	0.0267	0.1393	0.0087
45	9	0.0062	0.0240	0.1905	0.1359
42	10	0.0063	0.0234	0.1945*	0.1543
30	11	0.0046	0.0200	0.1928	0.2161
25	12	0.0038	0.0182	0.1821	0.2345
24	13	0.0037	0.0178	0.1791	0.2375
22	14	0.0034	0.0169	0.1722	0.2426
21	15	0.0032	0.0165	0.1684	0.2448
20	16	0.0031	0.0160	0.1642	0.2466
19 (2)	17-18	0.0029	0.0155	0.1596	0.2480
17	19	0.0026	0.0145	0.1496	0.2498
16 (2)	20-21	0.0025	0.0140	0.1441	0.2500*
14	22	0.0022	0.0128	0.1319	0.2489
13	23	0.0020	0.0122	0.1253	0.2475
12	24	0.0019	0.0116	0.1182	0.2455
10 (2)	25-26	0.0016	0.0103	0.1030	0.2390
9 (7)	27-33	0.0014	0.0096	0.0947	0.2343
8 (2)	34-35	0.0013	0.0088	0.0860	0.2285
7 (4)	36-39	0.0011	0.0080	0.0769	0.2212
6 (6)	40-45	0.0009	0.0072	0.0674	0.2123
5 (10)	46-54	0.0008	0.0063	0.0574	0.2013
4 (8)	55-62	0.0006	0.0053	0.0469	0.1874
3 (11)	63-73	0.0005	0.0043	0.0359	0.1695
2 (16)	74-89	0.0003	0.0031	0.0244	0.1454
1 (56)	90-145	0.0002	0.0018	0.0125	0.1093

frequencies are particularly large with both collections. As a consequence, significant differences in index values are to be attributed to an astonishingly low number of species. Beginning with the discussion of the general traits of sensitivity profiles, let us take as a typical example the sensitivity profile of the H index, based on the frequencies of the synanthropic flies. Sensitivity relating to the largest frequency 1442 is  $\Delta_{1442} = -0.8721$  (the point  $[\log 1442; -0.8721 / \Delta_{max}]$  has been omitted from the sensitivity profile). As compared with other sensitivity values relating to the frequency set, the absolute value 0.8721 is rather large. Index response  $\Delta_{244}$  belonging to the second largest frequency 244 is also negative, but its absolute value is quite small. That is, just a slight increase of that frequency also decreases the Shannon diversity (i.e., increases the degree of dominance in the multispecies population concerned). However, in this population the species involved rates as a nearly indifferent or quasi-neutral one. (In a

sense, the smallest frequencies should also be taken for nearly indifferent ones.) The index response relating to the third largest frequency 218 is already positive. That is, the slight increase of that frequency increases the diversity. However, the sensitivity is small, and in this population this frequency should also be considered a nearly indifferent one. Index sensitivities relating to all further frequencies are also positive. Thus, on that basis, we can define in the population *dominant* and *subordinate* frequencies, whether the increase of the frequency concerned yields an increase or decrease in the diversity. (The expression *dominant frequency* is frequently employed in the ecological literature without a clear definition.) As for the positive index responses, the largest value belongs to frequency 85. Consequently, the relative sensitivity profile reaches its maximum value 1 at  $\log 85$ . As for smaller frequencies, the sensitivity rapidly decreases. However, it should be noted that even the five percent increase of (the

continuous form) of frequency 4 results in almost as great an increase in the diversity, as does the identically proportionate increase of frequency 244 (Table 1). Moreover, the index response relating to frequency 1 is also significant, as compared with sensitivity relating to the second largest frequency (Table 1). Naturally, all of the latter sensitivities are small as compared to the largest sensitivity.

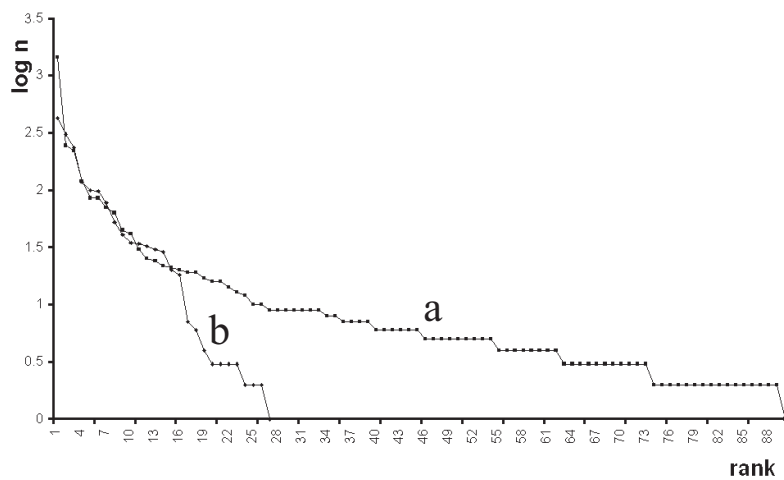
Considerable experience with earlier sensitivity studies and comparison of the sensitivity profiles in Figs. 2-3 and data in Tables 1-2 lead us to suggest that a characterisation of the sensitivity conditions for a fixed data set

should take account of the following sensitivity parameters:

- parameter *a*: the number of the dominant frequencies,
- parameter *b*: the number of frequencies between those to which belong the maximal positive and negative sensitivities  $\Delta_{max}$  and  $|\Delta|_{max}$ , respectively,
- parameter *c*: the value of  $\Delta_{max}$ ,
- parameter *d*: the sensitivity  $\Delta_1$  relating to frequency 1,

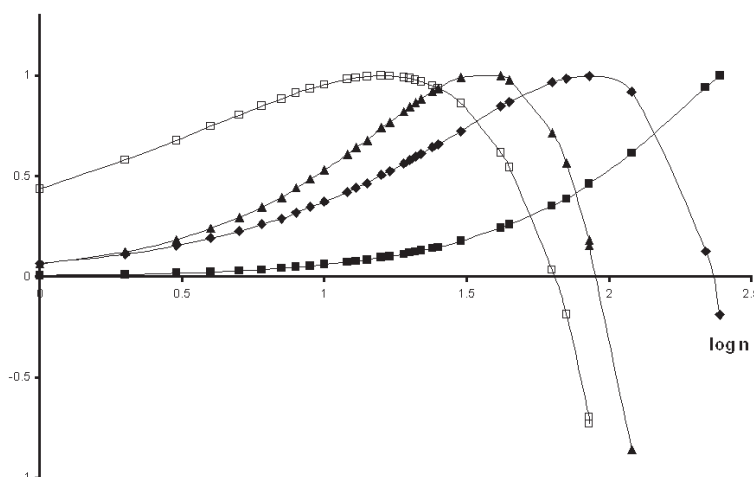
**Table 2.** Species abundances or frequencies and basic sensitivity data for drosophilid flies.\* and + as with Table 1.

sensitivity ( $\Delta_n$ )					
frequency ( <i>n</i> ) (with multiplicities)	rank ( <i>r</i> )	E <sub>2</sub>	H	E <sub>50</sub>	N <sub>0.5</sub>
424	1	-0.0592+	-0.2579+	-1.2269+	-2.0982+
306	2	-0.0175+	-0.1271+	-0.8849+	-1.2544+
237	3	-0.0021	-0.0626+	-0.6815+	-0.7893+
118	4	0.0088*	0.0175	-0.2407	-0.0774
99	5	0.0087	0.0249	-0.1342	0.0176
97	6	0.0086	0.0256	-0.1220	0.0271
78	7	0.0080	0.0306	0.0023	0.1118
53	8	0.0064	0.0329*	0.1758	0.2022
41	9	0.0053	0.0317	0.2455	0.2326
35	10	0.0046	0.0303	0.2701	0.2430
34	11	0.0045	0.0301	0.2732	0.2443
32	12	0.0043	0.0294	0.2784	0.2466
30	13	0.0041	0.0287	0.2822	0.2484
29	14	0.0040	0.0284	0.2835*	0.2490*
20	15	0.0029	0.0240	0.2722	0.2466
18	16	0.0026	0.0227	0.2630	0.2434
7	17	0.0011	0.0127	0.1487	0.1929
6	18	0.0009	0.0115	0.1317	0.1833
4	19	0.0006	0.0086	0.0937	0.1584
3 (4)	20-23	0.0005	0.0070	0.0726	0.1417
2 (3)	24-26	0.0003	0.0051	0.0500	0.1201
1 (5)	27-31	0.0002	0.0030	0.0258	0.0890

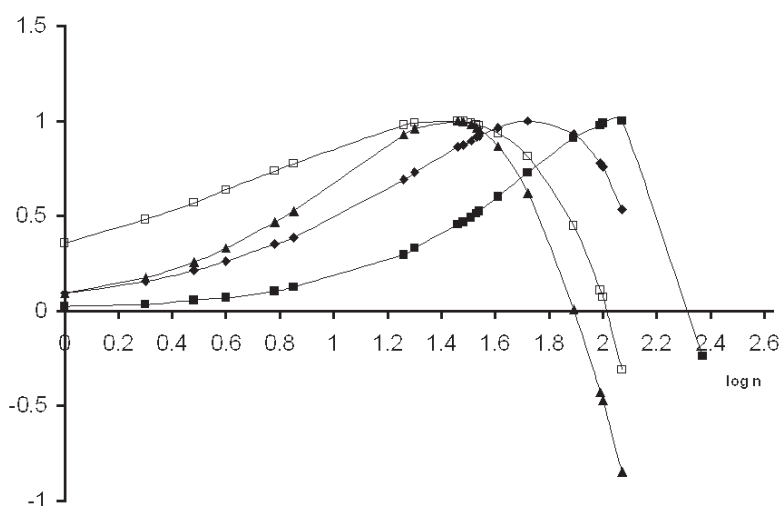


**Figure 1.** Decreasingly ordered species abundances on logarithmic scale. **a:** synanthropic flies, **b:** drosophilid flies.

**Figure 2.** Sensitivity profiles, synanthropic flies. Relative partial sensitivities ( $\Delta_{nk}/\Delta_{\max}$ ) are plotted against frequencies  $n_k$ . Symbols: ■:  $E_2$  index, ◆: Shannon index H, □:  $E_{50}$  index, ▲: Hill index  $N_{0.5}$ . Points not shown in the graphs,  $E_2$ : (3.16, -8.535); H: (3.16, -31.598);  $E_{50}$ : (2.34, -3.646); (2.39, -4.277), (3.16, -27.308);  $N_{0.5}$ : (3.16, -70.985), (2.39, -7.418), (2.34, -6.224), (2.08, -2.014).



**Figure 3.** Sensitivity profiles, drosophilid flies. Symbols as in Fig. 2. Points not shown in the graphs,  $E_2$ : (2.49, -1.989), (2.63, -6.727); H: (2.37, -1.903), (2.49, -3.863), (2.63, -7.839);  $E_{50}$ : (2.37, -2.404), (2.49, -3.121), (2.63, -4.328);  $N_{0.5}$ : (2.37, -3.17), (2.49, -5.038), (2.63, -8.427).



- parameter  $e$ : the ratio  $|\Delta|_{\max}/D(\mathbf{n})$ .

By inspecting the results in Tables 1-2 and the figures one can establish that the sensitivity conditions depend, among others, on the frequency set. On the other hand, for a fixed frequency set the above sensitivity parameters correlate. This has in part a theoretical basis. For example, for the  $E_m$  ( $m = 2, 3, \dots$ ) indices, we reported earlier (Izsák 1996) that by increasing  $m$ , the abscissa of the intersection of the profile and the horizontal axis positively correlates with the abscissa of the maximum site. This involves a positive correlation between sensitivity parameters  $a$  and  $b$ .

To determine whether parameters  $a$ ,  $b$ ,  $c$  and  $d$  correlate in the present case as well, we summarised these characteristic sensitivity parameters for each diversity index.

Indexing the parameters by the diversity index concerned, the data of the synanthropic flies yield:

$$a_{N_{0.5}} > a_{E_{50}} > a_H > a_{E_2}, \quad b_{N_{0.5}} > b_{E_{50}} > b_H > b_{E_2},$$

$$c_{N_{0.5}} > c_{E_{50}} > c_H > c_{E_2}, \quad d_{N_{0.5}} > d_{E_{50}} > d_H > d_{E_2}.$$

With Drosophilidae the ordering provides the same result, with the exception that  $a_{E_{50}} > a_{N_{0.5}}$  and  $c_{E_{50}} > c_{N_{0.5}}$ . The result suggests a general positive correlation between the sensitivity parameters  $a - d$ .

In the case of the sensitivity parameter  $e = |\Delta|_{\max}/D(\mathbf{n})$   $e_H$  exceeds  $e_{E_{50}}$  with both frequency sets:  $e_{N_{0.5}} > e_H > e_{E_{50}} > e_{E_2}$ . On the basis of the observed correlations, we can identify the index sensitivity for a fixed data set by a single parameter, say, by the number of the dominant frequencies (parameter  $a$ ). Then, as outlined above, we can



**Table 3.** Sensitivity parameters for different diversity indices in two samples of flies.

sensitivity parameters		synanthropic flies				drosophilid flies			
parameter code	description	$E_2$	H	$E_{50}$	$N_{0.5}$	$E_2$	H	$E_{50}$	$N_{0.5}$
a	number of dominant frequencies	1	2	4	7	3	3	6	4
b	number of frequencies between frequencies belonging to $\Delta_{max}$ and $ \Delta _{max}$	0	4	8	17	2	6	12	12
c	$\Delta_{max}$	0.0258	0.0276	0.1945	0.2500	0.0088	0.0329	0.2835	0.2490
d	$\Delta_1$	0.0002	0.0018	0.0125	0.1093	0.0002	0.0030	0.0258	0.0890
e	$ \Delta _{max} / D(n)$	0.1252	0.3370	0.3080	0.3738	0.0317	0.1069	0.0915	0.1274

say that the increase of sensitivity correlates with the increase of sensitivity parameters  $b - d$ , and possibly  $e$ .

Note that the observations clearly indicate that H depends on changes in the leading frequency to a lesser degree than do  $E_2$  and the Gini-Simpson index  $GS$ . This has been mentioned in the literature treating such numerical experiments (Magurran 1988, chap. 4) as well. However, our results show that H is also quite sensitive to changes in the leading frequency.

Having concluded the formal statistical analysis, we touch upon some ecological considerations. The quantitative sensitivity analysis presented above provides answers to the following questions:

- To what extent does the frequency of the most abundant species determine the value of diversity?
- Does a slight increase in the species abundance of a given species increase or decrease the diversity? On this basis one can identify the dominant and subordinate group of species relating to the diversity index used.
- What is the number of those large frequencies which practically determine the index value?
- Which are the species in a community the abundance of which can be altered to a small degree without causing an essential change in diversity (so called nearly indifferent species)?
- Furthermore, we should add that Pielou (1979) has suggested that the effort required to identify and count microscopic or taxonomically difficult organisms is high with regard to the usefulness of the achieved diversity estimates. Pielou recommends a

method for estimating the diversity on the basis of the abundances of the three most abundant species. Clark (1992) recommends extending the method to the  $n$  most abundant species, discussing results with  $n = 2, 3, 4$  and 5. However, this author also does not suggest a plausible value for  $n$ . With the knowledge of the sensitivity conditions obtained by our sensitivity analysis, it is easy to specify the number of the species or largest frequencies, to which diversity calculations should be restricted. For example, in the treated collections of synanthropic flies and of Drosophilidae, this number for H is 1 and 3, respectively.

Owing to the determining role of some large frequencies, in a wider sense, all species with smaller frequencies rate as nearly indifferent species. This fact is somewhat disappointing, as an early concept of diversity suggested that the diversity index value is a joint product of numerous species abundances in a community. The outlined quantitative method shows that this is decidedly not the case.

All of these methodological possibilities can facilitate the development of a more flexible means of representation with respect to the relations between changes in the community structure and diversity.

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