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Diversity, diversity indices and tropical cockroaches

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Summary. The diversity of samples of cockroaches (Blattaria) taken with light-traps in six localities in Panama is described. As a diversity index α of the log series is found to be more satisfactory than either N_2 or N_1 of Hills's series or Hurlbert's S_m, even if the distribution of the relative abundances is significantly different from a log series. However, even the α-index is of only limited usefulness. A simple statistic such as the number of species per unit effort can be at least as useful. The seasonal variation in the value of the diversity indices is negatively correlated with both the number of species and the number of individuals. Mountain sites have a lower alpha-diversity than lowland sites and relatively undisturbed sites have more individuals and more species than disturbed ones, although this difference is not reflected in the value of the diversity indices. To describe the beta-diversity the NESS similarity index, here called C_m, is far superior over any other indices available. The between site diversity is very high. Samples taken at the same site in successive years in most cases are significantly different from being random samples of the same fauna.

1. Introduction

The diversity of tropical insects has fascinated biologists ever since the first explorers published their experiences in a tropical rainforest. There is little doubt that there are more species of insects in the tropics than in temperate areas in most groups, with the possible exception of some parasitic Hymenoptera (Owen 1974; Owen et al. 1974; Hespenheide 1979; Morrison et al. 1979; Janzen 1981) and bees (Michener 1979). There is considerable confusion, however, on the absolute and relative abundances of these species. Elton (1973, 1975), like many others, was impressed by the very low population densities inside a neotropical rainforest, with only a few exceptions such as ants and some small Diptera. Owen (1966) on the other hand, concluded for tropical Africa that while there was a large number of rare species, that "some common species may be as common as comparable species in the temperate regions". The latter view was already given by Bates (1892, cited by Taylor 1978) and is supported by evidence given by Gray (1972) and Wolda (1978b) about insects reaching outbreak proportions in a tropical forest.

What, then, are the relative abundances of species in a tropical forest? Does their distribution resemble that found for temperate insects, i.e. roughly follow a log series or log normal distribution, or is their some fundamental difference apart from the larger number of species? Is the alpha (=within site)- diversity different in different localities within the tropics? Does it vary, for instance, with the degree of human disturbance the habitat has experienced? Is the beta diversity (differences between sites (Whittaker 1960)) in the tropics also relatively large?

When trying to answer questions such as these, a major problem arises: the technical problem of how to deal with diversity. Which, if any, of the diversity indices which abound in the literature can profitably be used? The present paper deals mainly with this problem, using a set of light-trap samples of tropical cockroaches (Blattaria) collected in six localities in the Republic of Panama. These data will also be used to compare the six sites using similarity indices.

2. Materials and methods

Light-traps were installed for various lengths of time in a number of localities in Panama. The traps are modified Pennsylvania black-light-traps. On Barro Colorado Island (BCI), in Las Cumbres and in Boquete they operated every night, all night. In Fortuna, Miramar and Corriente Grande they operated every night from dusk until 10 p.m..

Barro Bolorado Island (BCI), 9°9′19″N; 79°45′19″W, is an island in Gatun Lake in the Panama Canal area. The traps are at 120 m above sealevel in relatively undisturbed forest (Croat 1978). One is near ground level and one in the canopy, 2 and 28 m above the forest floor respectively. Cockroach samples are available from early 1975 to early 1981.

Las Cumbres, 9°5′36″N; 79°31′54″W, is a residential area, with gardens and some second growth forest (Wolda 1980), some 16 km North of Panama City. Cockroach samples are available from 1974 through 1976. Altitude 150 m.

Boquete, 8°48′N; 82°26′W, altitude 1,350 m, is in the mountains of Western Chiriquí province. The trap was in the community Alto Lino, in a small forest remnant among coffee plantations. Cockroaches were taken from the light-trap samples from January 1976 to July 1978.

Fortuna, 8°44′N; 82°16′W, altitude 1,050 m is in a wet mountain valley some 20 km East of Boquete. A trap was operated here from September 1976 until July 1979, the first nine months at canopy level, the last two years at some 3 m above the forest floor, in relatively undisturbed forest. For details of the area see Adames (1977).

Miramar, 9°N; 82°15′W, sea level, is in the province of Bocas del Toro in NW Panama, on the coast of the Laguna de Chiriquí. From November 1978 through November 1979 the trap was located at the edge of a pasture at the bottom of a forested slope with mostly cacao in the undergrowth.

Corriente Grande, 9°17′30″N; 82°32′41″W, altitude 100 m, is on the Rio Changuinola, some 60 km NW of Miramar. The trap was operated from January to May 1980 in forest from which recently some timber trees had been removed.

In BCI, Las Cumbres and Boquete there is a clear alternation of an 8-month rainy season and a 4-month dry season, the latter occurring from January through April. Annual rainfall is around 1,500 mm in Las Cumbres and 2,500 mm in BCI and Boquete. In Fortuna mean annual rainfall is almost 5,000 mm with no dry season, i.e. the precipitation per month does not predictably vary over the year. In Miramar and Corriente Grande there are no weather records, but extrapolating from some weather stations elsewhere in the province, the annual total estimated for Miramar is 3,000 and for Corriente Grande 2,500 mm. Again there is no dry season in either site, but both March and September tend to have less rain than the other months of the year.

Alpha – diversity

The within-site or alpha-diversity (Whittaker 1960) is often described by a single parameter, a diversity index. Fisher et al. (1943) used the parameter α of the log series to describe the diversity of a sample. The distribution of the relative abundances of the species in the sample is then assumed to follow the log series distribution. Others have invoked other theoretical distributions, such as the broken stick model, the log normal etc., and used the parameters of these as diversity indices. Many diversity indices have been developed which do not assume some theoretical distribution and as such seem more attractive. Among these the Shannon-Weaver index ($H' = -\Sigma(p_i \ln p_i)$) has enjoyed great popularity. However, objections to this and other indices have been raised because of their strong dependence on sample size, their biased estimators, their dependence on the few most common species in the sample etc. Some critics have gone so far as calling diversity a non-concept (Hurlbert 1971). May (1975a, b) states that one should not expect a single parameter to describe adequately the diversity of a sample and suggests that information on the actual distribution of species abundances is needed, which may require more than one parameter. However, the quest for more acceptable indices has continued. Hill (1973) describes a family of diversity indices N_i with N_1 equal to $\exp(H')$ and N_2 to the reciprocal of Simpson's index, i.e. $1/\Sigma p_i^2$. Several authors strongly prefer N_2 over all other indices, with N_1 a distand second (Peet 1974, Alatalo and Alatalo 1977, Routledge 1979). Smith and Grassle (1977) and Smith et al. (1979) developed a generalization of the Simpson's index S_m, where any value can be selected for m and which for higher values of m becomes increasingly sensitive to the rare species. The basic formula for S_m is $S_m = \Sigma(1-(1-\pi_i)^m)$. S_m has an unbiased estimator which is $\Sigma\, 1 - C(n-n_i, m)/C(n/m)$, which is the index proposed by Hurlbert (1971). Here S_m is the number of species expected in a sample of m individuals selected at random from a collection containing n individuals, S species and n_i individuals in the i_{th} species. π_i is the proportion of the i_{th} species in the universe which was sampled.

The original log series parameter, however, was strongly defended by Kempton (1975; 1979), Taylor (1978), Taylor et al. (1976) and Kempton and Taylor (1979). There are strong arguments against the use of an a priori distribution such as the log series. It only makes sense if indeed the log series adequately describes the distribution of the individuals over the species in all samples under consideration. In practice in many cases no significant deviation from the log series was observed, but unless both the number of species and the number of individuals are large, it may be very difficult to demonstrate such a deviation (Peet 1974). However, even more important than the fit of the data to a theoretical distribution is the behaviour of the index in practice. Taylor et al. (1976) compared the behaviour of the α of the log series with modifications of the N_1 and N_2 indices. They demonstrated that both N_2 and N_1 are strongly affected by the most abundant species, much more so than α, and that α should be given preference over these indices of the Hill series, even in cases with a moderate deviation from the log series distribution.

In present paper I will use the four indices α, N_2, N_1 and S_m, where I chose the value of 20 for m. These, to the best of my knowledge, are the best indices available at this moment. I will test which, if any, of these is helpful when studying diversity.

Beta – diversity

Whittaker (1960) used the term beta – diversity for differences between faunal of floral samples or for changes in community structure over time. Such problems can best be studied using similarity indices. A large number of these have been developed in the last 60 years or so, but some recent developments have cleared up the confusion considerably, Jansen and Vegelius (1981) compared a large number of binary indices (for presence-absence data) and concluded that only three of them, viz. the Ochiai, the Jaccard and the Czekanowski (= Sørensen) index (the latter ascribed to Dice by Janson and Vegelius) are worth considering at all. For these three indices they developed large sample estimates of a variance which allow the use of such indices in hypothesis testing. Unfortunately, to the best of my knowledge, all binary indices, including the ones favored by Janson and Vegelius, are biased in that the expected value for two random samples drawn from the same universe is less than unity, the more so if the samples are smaller and the diversity is larger (Wolda 1981). Because the Jaccard index is non-linear according to a criterion used by Wolda (1981), that index should be deleted from the list also for this reason. I have shown (Wolda 1981) that of all the non-binary similarity indices (i.e. the ones which do take the relative abundance of the species into account) only one, the Morisita index (Morisita 1959) is unbiased. A disadvantage of that index is that it depends heavily on the most common species. However, Grassle and Smith (1976) developed a generalization of the Morisita index. Their new measure is called the Normalized Expected Species Shared (NESS) between random samples of size m drawn from a population. The larger the value of m, the less NESS becomes dependent on the most common species. At $m = 1$ NESS is equal to the Morisita index. At any m, NESS is unbiased. The designation NESS is a bit

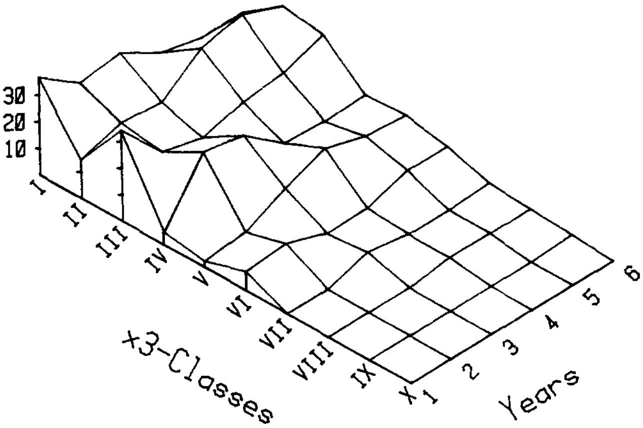

Fig. 1. Frequency distribution of the number of individuals per species of cockroaches collected on Barro Colorado Island. Abundances are given in $\times 3$ classes, i.e. classes with upper limits 1.5 for class I, 4.5 for class II, 13.5 for class III ect. Frequencies, given in percentages, for the first year (year 1 = 1975), the first two years combined, the first three years combined etc. The distribution differs significantly from a logseries in that it is bimodal

awkward so I propose "C_m" be used in reference to Morisita's C_λ. At a number of values for m the index was tested using a number of simulated insect faunas taken randomly from a log series distribution with four different values of the diversity index α (see Wolda (1981) for details on these simulated faunas). These simulations confirmed the results by Grassle and Smith that C_m is unbiased and that the expected value for two random samples taken from the same universe is abount unity and independent of sample size and diversity.

The next major step was made when Smith et al. (1979) published a technique for estimating the variance of C_m. This means that this unbiased index (the only one in existence as far as I know), which is not overly affected by the most common species, can be used for testing hypotheses. This makes it far superior over all other indices.

Throughout this paper the value of m in C_m shall be 20 to assure a reasonably large influence of rarer species.

Results

In most cases the distribution of individuals among species in the cockroach samples is not significantly different from a log series, except at BCI where it is bimodal. This is illustrated in Fig. 1 where the distribution, in x3-classes, i.e. 1, 2–3, 5–13, 14–40, etc. individuals per species, is plotted for the first year (1975), the first two years combined etc. until all six years combined, in a threedimensional plot. One of the two peaks was at class I in 1975, moved to class II after 4 years and covered class II and III after 6 years. The second peak was at class III (5–15 individuals per species) in 1975 and moved to classes V and VI after 5 years. This general pattern shows that the biomodality is real and not a freak accident of a given moment. In spite of this biomodal distribution, which is significantly different from the log series, α is calculated along with the other diversity indices and given in Table 1 for the yearly totals (in three of the 17 cases the period is less than a full year). The three indices, N_1, N_2 and S_{20} are highly correlated (Table 2a) with values of the correlation coefficient around 0.94. This means, that, at least for this set of data, the three indices convey equivalent information, even though N_2 is supposed to be much less sensitive to the rare species N_1 (Peet 1974; Hill 1973; Alatalo 1981)

Table 1. Diversity of samples of cockroaches collected with light-traps in six localities in Panama. N = number of individuals, S = number of species, and the diversity indices α, N_2, N_1 and S_{20}. Unless otherwise indicated, each sample covers a full year

	N	S	$\alpha + \pm$st.dev.	N_2	N_1	S_{20}
Barro Colorado Island						
1975	864	43	9.52±1.45	6.53	11.29	8.70
1976	507	36	8.85±1.48	9.66	15.12	10.40
1977	1,438	53	10.82±1.49	7.56	13.74	9.57
1978	3,224	79	14.62±1.66	5.46	11.44	8.69
1979	2,932	59	10.46±1.36	6.21	8.88	8.36
1980	2,421	49	8.70±1.24	5.51	10.05	8.16
Las Cumbres						
1974	324	30	8.08±1.48	8.88	13.68	10.29
1975	342	39	11.33±1.82	8.11	14.60	10.47
1976	385	32	8.28±1.47	9.06	14.49	10.52
Miramar						
1979	182	30	10.24±1.87	8.32	13.38	10.29
Corriente Grande						
1980 (4 months)	370	44	13.02±1.96	15.75	23.25	12.88
Boquete						
1976	77	12	4.00±1.15	3.33	5.69	7.18
1977	65	14	5.46±1.46	6.53	8.90	8.83
1978 (6 months)	45	14	6.99±1.87	5.74	8.66	9.51
Fortuna						
1976/77 (9 months)	170	20	5.88±1.32	8.06	10.82	9.10
1977/78	659	30	6.47±1.18	7.31	12.57	9.89
1978/79	1,037	33	6.49±1.13	5.27	9.98	8.84

or S_{20} (Smith and Grassle 1977; Smith et al. 1979). The correlation of α with the other three, however, is much lower. This is almost entirely due to the six years of data from BCI, within which the correlation between α and the other indices is negative. When the BCI datapoints are excluded, the correlations of α with the other indices are much higher $(r(\alpha,N_2)=0.818,\ r(\alpha,N_1)=8.93,\ r(\alpha,S_{20})=0.908$. This is exactly what one might expect considering the fact that the BCI samples did not follow the log series. However, that is not the explanation.

In Fig. 2 S_{20} is plotted against α to illustrate the discrepancy between the indices. Plots of N_1 or N_2 against α give similar results. The non-BCI data are in a narrow band with the Boquete and Fortuna samples less diverse than the other sites and the Corriente Grande sample by far the most diverse. According to the α-index (abscissa) BCI was, on the average, about as diverse as Las Cumbres and Miramar, although there was a considerable variation between years. The 1978 BCI sample was, according to α, the most diverse sample in the set. According to the other three indices (S_{20} along the ordinate as an example) almost all BCI samples, including the 1978 sample, are as poor as the mountain sites Fortuna and Boquete. The highest diversity at BCI, as measured by these other indices, is the 1976 sample, which reaches the level of Las Cumbres and Miramar samples. This is rather confusing. However, when going back to the original data (Table 1), one sees that on BCI 1978 was, in fact, the richest sample both in individuals and in species. The 1976 BCI sample, on the other hand, was rather poor. It seems, therefore, that the α-index provides information which is intuitively better than that of the other indices. Taylor et al. (1976) observed a similar phenomenon, which they attributed to the extreme sensitivity of their versions of N_1 and N_2 to the most abundant species. In Fig. 3 the plot of S_{20} (N_1 or N_2 give similar results) against α is repeated for the BCI data with the two most abundant species (*Panchlora* sp. and *Chromatonotus heterus* Hebard) omitted. The deletion of these two abundant species improves the correlation considerably and brings the BCI points inside the narrow band of points for the data from the other sites (Fig. 2). When omitting these two species in 1978 N_2 increased from 5.46 to 15.71 and N_1 from 11.44 to 26.12, which shows that these indices are even more sensitive to the most abundant species than S_m. One might think that 20 is too low a value for m to make S_m sufficiently insensitive to the most common species. However, even with $m=100$ the situation is not realy improved. This points to the conclusion that all three indices S_m, N_1 and N_2 are much more sensitive to the most common species than α of the log series even in this case where the log series is not a good fit for the data. This confirms and extends the conclusion by Taylor et al. (1976) that for most cases α is the best index available.

The conclusion then is, that the two mountain sites Boquete and Fortuna do not differ much in diversity but are less diverse than Las Cumbres, BCI and Miramar which also are very similar in diversity with the exception of BCI 1978 which is the most diverse sample at hand. Corrient Grande is very diverse too, especially if one takes into account that it represents only four months of the year. These conclusions, however, tell only part of the story, being based only on α. Table 1 shows that the Boquete samples are actually much poorer than those from Fortuna and Miramar, and, to, some extent, Las Cumbres are

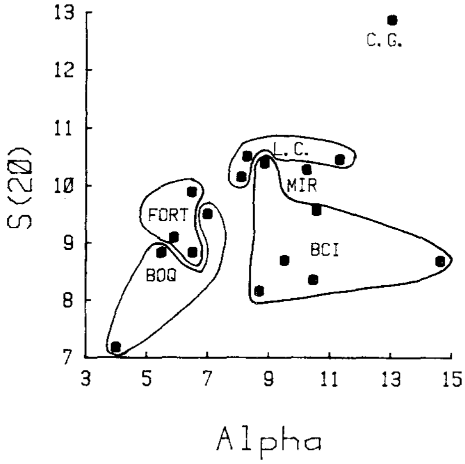

Fig. 2. Scatterplot of the values for two diversity indices, S_{20} and α, showing the rather different results of these indices. *C.G.* Corriente Grande, *L.C.* Las Cumbres, *Mir* Miramar, *Fort* Fortuna, *BCI* Barro Colorado Island, *Boq* Boquete

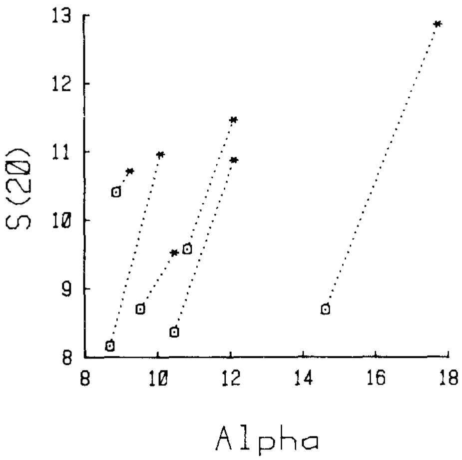

Fig. 3. Scatterplot of the values of two diversity indices for cockroaches from BCI with all species included (squares) or with the two most common species omitted (*)

poorer than BCI. A collector who is interested in large numbers of individuals and a great variety of species would go to BCI and Corriente Grande rather than the other lowland sites and to Fortuna rather than Boquete, whatever the diversity index says. The α-index may be the best diversity index available, it is not ideal.

There is a clearcut seasonal variation in abundance and occurrence of species of cockroaches, even in relatively "non-seasonal" sites (Wolda and Fisk 1981). How does the diversity vary over the seasons? Taylor (1978) shows, for a set of British moths, that as the number of individuals and the number of species reach their seasonal peaks, so does the diversity index α. This was studied with the BCI data by taking the information per period of four weeks. In the first two years the number of individuals caught was rather low so that the diversity indices are unreliable. In subsequent years, however, the numbers caught increased sufficiently for the analysis. The correlations between the four indices is given in Table 2b, showing that

Table 2. Correlation between diversity indices α, N_2, N_1 and S_{20} for cockroaches collected in Panama with light-traps. **a)** yearly samples (Table 1, $n=17$) and **b)** samples per 4 weeks on Barro Colorado Island ($n=81$, Fig. 4)

	N_2	N_1	S_{20}
a) α	0.433	0.592	0.441
N_2	–	0.950	0.937
N_1	–	–	0.939
b) α	0.708	0.747	0.791
N_2	–	0.919	0.858
N_1	–	–	0.903

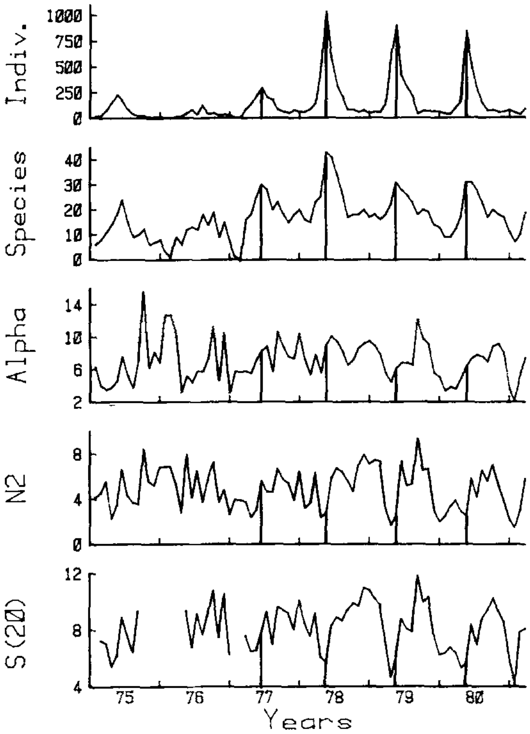

Fig. 4. Seasonal variation in diversity of cockroaches from BCI. Data given per four weeks throught 6 years of collecting. For the last four years, when the samples were reasonably large, he peak in number of individuals and that in species is accentuated with a vertical line, also in the index plots. As diversity indices the α of the log series, N_2 of Hill's series and S_{20} of Hurlbert are used. The graph for N_1 is not included as it is very similar to that for N_2 and does not give any extra information.

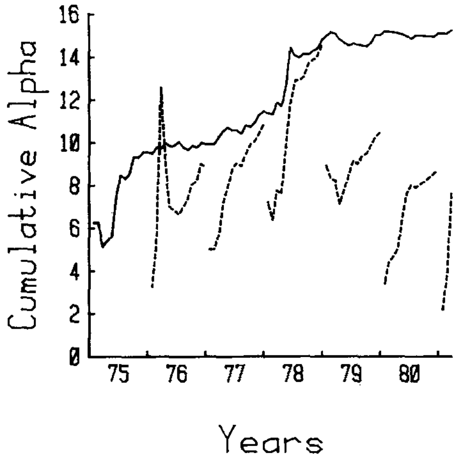

Fig. 5. Diversity on BCI, as measured by α, per four weeks, cumulative over each year (dashed lines) and over all 6 years (solid line). The two linetypes are identical in the first year.

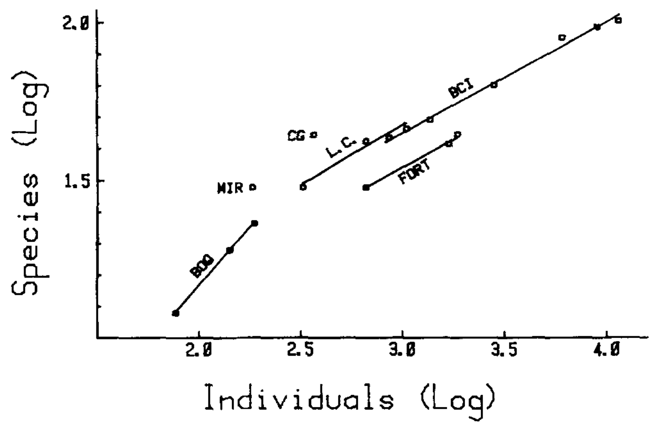

Fig. 6. The number of species plotted against the number of individuals on a double-log scale. For those sites where more than one year is available, points are given for the first year, the first two years combined, etc., and these plots are represented also by a regression line. *BCI* Barro Colorado Island, *L.C.* Las Cumbres, *FORT* Fortuna, *C.G.* Corriente Grande, *MIR* Miramar and *BOQ* Boquete

at these smaller sample sizes N_1, N_2 and S_{20} are still highly correlated and the correlation of these with α is lower. Seasonal fluctuations in the indices are plotted in Fig. 4. Just as there is a clear seasonal variation in the total number of individuals and the number of species, there also is one in the value of the indices. The peak in the number of individuals (accentuated by vertical lines in Fig. 4) roughly coincides with a peak in the number of species, but also with a low in the index values. At the beginning of the rainy season, around late April, the number of individuals increases faster than the number of species, causing a low value for the indices. After that the number of individuals drops rather dramatically and much faster than the number of species, which causes a peak in the indices. There is a tendency for a second, low, peak of the indices in the dry season when the number of individuals are low but there are still several species present as adults. This is very different from the seasonality observed in British moths where a peak in the index coincided with a peak in individuals and species (Taylor 1978). The seasonal variation in diversity can best be described by describing changes in individuals and species, as I just did, but leaving out any reference to the diversity indices. Including the indices does not give any extra information or clarification.

The value of a diversity index depends very much on the period covered by the sample, because of seasonal and yearly variations in the abunandes of the species concerned. This is also true for these tropical samples. In Fig. 5 the α-index is plotted for cumulative samples from BCI within each year and for all six years combined. The values are for the first period of 4 weeks, the first two periods, etc. The result is that after some initial variation in values, due to small sample size, the value of α increases as the year goes by. It also increases, and keeps increasing, over the total 6-year period. The number of new species (=not found before at this site) is sufficiently large not to permit the larger number of individuals to stabilize or lower the value of the diversity index.

An old and simple way of looking at diversity is by means of "discovery curves", where the number of species is plotted cumulatively against the number of individuals. This is done, on a double-log scale in Fig. 6. For those sites where there is more than one year of data a plot is given for the first year, the first two years combined etc., and these plots are then represented by a linear regression line. All four lines have a slope larger than expected on the basis of a constant α. The further one moves to the right on any one of these lines, at higher the diversity as measured by α. At any number of individuals the sample with the largest number of species is the most diverse. In Fig. 6 that means that Corriente Grande is more diverse than Las Cumbres, that Las Cumbres is about as diverse as BCI and that Fortuna is less diverse. Extrapolating any lines to Boquete and Miramar is tricky and might better be avoided. The conclusions are similar to the ones obtained with the α-index, although there Miramar and Boquete could be included. Figure 6, however, does include the extra information about the number of species and individuals obtained per unit time. After one year of sampling many more individuals and species were obtained in Fortuna than in Boquete and Miramar had many fewer individuals but the same number of species as Fortuna. The sampling was done in exactly the same way in these three sites so this translates to the number of species and individuals per unit effort. Corriente Grande was different in that the trap was operated only for four month, which emphasizes the richness of the fauna there. In Las Cumbres the trap operated all night in stead of only to 10 p.m. which should mean that more individuals were caught than would have been the case had the trap operated only until late in the evening. After one year in Las Cumbres about the same number of species were caught as in Fortuna, but with fewer individuals. Two years in Las Cumbres were needed to equal the number of individuals in one year in Fortuna, but by that time there are more species in Las Cumbres. Comparisons with BCI, where two traps functioned simultaneously all night, are difficult, but the fact that more individuals were caught on BCI in the first year than in two years in Las Cumbres and that the lines for BCI and Las Cumbres are virtually identical in slope and level suggest that the fauna on BCI is indeed richer than in Las Cumbres. In the study of diversity a plot like Fig. 6 may be as helpful, if not more so, than an index.

Table 3. Similarity between two successive years at the same site of cockroaches collected with light-traps. The index (C_{20} = NESS with $m=20$) is given ×1,000 and also the standard deviation ×1,000. Incomplete years are indicated by an asterisk

	C_{20}	95% limits
Barro Colorado Island		
1975 vs 1976	798±20	758–837
1976 vs 1977	934±18	898–971
1977 vs 1978	973±12	948–997
1978 vs 1979	941±7	927–954
1979 vs 1980	979±5	969–990
Las Cumbres		
1974 vs 1975	936±24	888–983
1975 vs 1976	976±17	942–1,011
Boquete		
1976 vs 1977	782±75	631–933
1977 vs 1978*	907±134	640–1,175
Fortuna		
1976/77* vs 1977/78	866±57	751–980
1977/78 vs 1978/79	910±16	879–941

Beta-diversity can be considered the complement of the similarity expressed by a similarity index, for which I use C_{20}, which is NESS with $m=20$ (Grassle and Smith 1976). However, before comparing different sites, it is worth-while to examine samples taken in successive years at the same site (Table 3). If the 11 values available, 9 are significantly different from unity, demonstrating that successive yearly samples cannot be considered random samples of the same community, but that there are real changes in the relative abundances of species within the community. Considering the results of many population dynamical studies this should come as no surprise to anyone, but it has rarely been demonstrated using a community statistic. The only study I am aware of trying to do this is Grossman et al. (1982) for stream fishes. They come to the same conclusion, although I find it hard to go along with their interpretation of this conclusion in terms of equilibrium or non-equilibrium status of the community. Because of these differences between years at the same site, one has to make decisions about what to use as a base for inter-community comparisons. Year 1 at site A compared with year 1 of site B may well give a result different from year 2 at site A with year 1 (or 2) of site B. It simply means that the value of the similarity index depends on the samples one happens to

Table 4. Similarity between samples of cockroaches taken with light-traps in six different localities in Panama. Values of C_{20} (=NESS with $m=20$) given ×1,000 with st. deviation ×1,000

	BCI	Las Cumbres	Miramar	Corr. Grande	Boquete	Fortuna
Indiv.	11,386	1,051	183	370	187	1,866
Species	100	47	30	44	23	44
C_{20}						
BCI	–	741±18	399±26	289±23	228±22	6±1
Las Cumbres		–	352±32	291±23	247±28	57±10
Miramar			–	427±42	212±30	52±18
Corr. Grande				–	82±20	99±21
Boquete					–	370±52

have available and the results should be viewed with some legitimate scepticism. I decided to us all the information at hand and characterize each site by the sum total of all yearly samples available. This should not statistically effect the value of C_{20} as it is independent of sample size.

The results, given in Table 4, show low between-site similarities. The highest similarity is between the two Central Panamanian lowland sites BCI and Las Cumbres and that is only 0.74. In general it can be said that most sites tend to be so different that they have very little in common. The extreme is Fortuna which is very different indeed from all other sites, including Boquete which is only 20 km away. In other words, there is a very high between-site diversity. Unfortunately, cockroaches are a predominantly tropical group and no sifficient temperate zone samples are available to make a direct comparison. However, it may very well be that in the tropics not only the alpha diversity, but also the beta diversity is much higher than that generally observed in temperate areas. Over 50 per cent of the 164 species of cockroaches were found in one locality only and these are not only species which are represented by only a few individuals (Wolda et al. in prep.) suggesting a high degree of endemism. Data on othergroups of insects will have to be studied to test this hypothesis.

Discussion

In a rich and complex environment with many factors affecting the insect populations, one expects the distribution of relative abundances to be similar to a log normal (May 1975a, b). The environmental conditions seem to be fulfilled in a tropical forest, but the cockroach samples do not follow the log normal distribution, not even on BCI where after six years over 11,000 individuals belonging to 101 species were collected. The observed distribution (Fig. 1) is bimodal and it is tempting to speculate that it is a composite of two log normal distributions of two different sets of species. A light-trap attracts nocturnal species. At present I have no way of knowing whether the samples obtained are representative of the flying nocturnal species in the forest. Probably not, though it might be close. There are, however, other species, even if one discounts the apterous species (Fisk 1982). Gradwohl (pers comm) collected a small sample of cockroaches on BCI using a very different technique and 46 per cent of her individuals belong to species not yet observed in the light-trap. This category, called "diurnal" for lack of a better term, may occasionally enter the trap. There are probably also species not resident in the area which are caught as they happen to pass the traps on their dispersal flight. Given the high beta-diversity in the tropics (Table 4), this category could be much more important than it is in the temperature zone. Unfortunately we know far too little about the basic life history of these cockroach species to be able to identify this category with certainty. However, such insect dispersal certainly exists in the tropics. The moth *Zunacetha annulata*, during specific times of the year, is caught in traps far from their normal habitat (Wolda 1978b) and so are hairstreak butterflies (Robbins and Small 1982). I hypothesize that the first mode in the BCI distribution (Fig. 1) is made up primarily of diurnal and vagrant species which the second peak represents mostly resident noctural species. However, other explanations can not be excluded at this stage. In one set of British moths an "unexplicable" bimodality was observed (Taylor 1978) which was apparently not caused by vagrants.

The cockroach fauna of Panama is very rich. A total of 164 species has been caught with the six light-traps discussed here, and there represent only part of the species in existence in Panama, a country the size of South Carolina or the Benelux. Several more species have been recorded from this country (Fisk and Wolda 1979; Fisk 1982) and in all likelyhood many more yet remain to be discovered. Large areas of Panama have not yet been sampled adequately and considering the large between-site diversity, it is likely that a high percentage of the fauna is still unknown to science. The number of species in Panama could easily exceed 300, although this number is probably diminishing as the natural habitats disappear. The entire United States and Canada only have 55 species (Helfer 1963), Texas has 31 species (Hebard 1943, Illinois only 14 (Hebard 1934), Michigan 9 (Cantrall 1963, Minnesota 5 (Hebard 1932) and North Dakota only 2 introduced species (Hebard 1936).

A simple and intuitively clarifying way of looking at diversity is to consider the number of individuals and species obtained per unit effort. In Table 1 a unit of effort is the collection by a light-trap during one year. Not all these samples can thus be directly compared because of some complications, such as two traps on BCI and one in the other sites, and traps operating all night (BCI, Las Cumbres, Boquete) or only from dusk to 10.- p.m. (Fortuna, Miramar, Corriente Grande). The Corriente Grande sample represents only four months. However, some of the sample can thus be compared and as a diversity index I favour one which gives the same impression as the number of species per unit effort. Among the indices tested the α of the log series in this sense is better than the other indices. E.g. the BCI 1978 sample was very rich and the only index which reflects this fact clearly is α. Taylor (1978) used, as a criterion to evaluate some diversity measures, their ability to distinguish between sites, their performance in an analysis of variance. His data, Taylor says, are inadequate to use the result as more than a provisional indication of general priorities. He had only four years for nine sites. I have only four sites with more than one year of data and in these sites 6, 3, 3 and 3 years. This is far less adequate than Taylor's dataset, but as each little bit may help, I present the results of both a one-way ANOVA and the parameter free Kruskal and Wallis test in Table 5. The suggestion here is that α discriminates better than the other indices tested. S_{20} does not show a significant difference between sites and N_2 is doubtful. Both N_1 and α demonstrate highly significant differences, with α possibly having the highest discriminatory abilities. This strengthens Taylor's conclusion that α is preferable. However, in the present case S, the number of species, is even better than α, which was not the case in Taylor's study.

Table 5. The ability of some diversity measures to discriminate between sites as measured by a one-way ANOVA (F-ratio) of a Kruskal and Wallis test (H). Sites included are BCI, Las Cumbres, Boquete and Fortuna

	S	α	N_2	N_1	S_{20}
F-ratio (3;11 df)	10.3	6.99	3.70	6.45	3.23
H (3 df)	11.78	10.60	5.71	8.36	6.96

If it is desirable to characterize the diversity of a sample with just one statistic, α compares favorably with the other statistics tested. However, it should not be used indiscriminately as it does not always seem to perform well. With May (1975a, b) I suggest that some extra information such as the relative abundances of the species (Fig. 1) or a species-individuals plot (Fig. 6) be included. In other cases, such as the seasonal distribution of diversity (Fig. 4) the use of an index does not help at all and should be avoided.

Data from only six sites are available and these sites differ in many aspects. However, it seems safe to hypothesize from the results that lowland areas tend to be richer in species than mountain sites and that disturbed sites tend to be poorer in both individuals and species than comparable undisturbed sites (Miramar vs Corriente Grande, Boquete vs Fortuna and Las Cumbres vs BCI).

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