Between-site similarity in species composition of a number of Panamanian insect groups

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Between-site similarity in species composition of a number of Panamanian insect groups.– The between-site faunal similarity has been studied in 12 groups of tropical insects, collected by light-traps, at seven sites in the Republic of Panama and was compared with some data sets from the literature, both from the temperate zone and from the tropics. There were large between-site differences in faunal composition, especially in relation with altitude. All insect groups were very similar in their between-site differences, suggesting that studying large segments of the fauna may be unnecessary for comparing sites and that the study of one or a few insect groups may suffice. The differences among tropical Panamanian sites tend to be larger than those in the temperate zone for most insect groups. However, great caution is required when comparing tropical and temperate inter-site similarities as data from the literature show that this may not be a universal trend.

Key words: Tropical Insects, Between-site similarity, NESS-index, Panama, Tropical-temperate comparisons.

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Introduction

Tropical insect faunas are extremely rich in species in most taxa, with some exceptions such as parasitic wasps (Gauld, 1987; Janzen, 1981; Owen, 1974), bees (Michener, 1979), and anthicid beetles (Wolda & Chandler, 1996).

This diversity varies among sites and depends, among other things, on the habitat, the history of disturbances, and altitude (Wolda, 1987). Less is known about variation in species composition and relative abundance between different sites. Any insect collector knows that for certain species one has to concentrate on certain sites and that faunas at different sites tend to differ. Rarely, however, have such differences been properly quantified.

For a few tropical groups, such as cockroaches (Blattaria), weevils (Curculionoidea), and Pselaphid beetles the between-site diversity is impressive (Wolda, 1983; Wolda et al., 1996; Wolda & Chandler, 1996), but more data are needed to study the amount of between-site similarities in faunal composition in general, to examine whether or not different insect groups are alike in their between-site similarities and to compare tropical and temperate data.

The present paper explores these questions using all the available data on twelve insect groups collected by light-traps at up to seven localities in Panama. Comparisons with the temperate zone will be made using a variety of data gleaned from the literature.

Methods

The tropical data

Light-traps were operated at seven sites in the Republic of Panama. Four of these are in the lowlands, namely Barro Colorado Island (BCI) in relatively undisturbed forest, and Las Cumbres, on the patio behind my house overlooking an area rich in trees with secondary forest nearby, both sites in Central Panama, and Miramar near coastal pasture and Corriente Grande in recently selectively logged forest, both in North-western Panama. Three sites are in the mountains of Western Panama, namely Fortuna in good forest at 1,050 m, Boquete in a forest remnant among coffee plantations at 1,350 m, and Guadalupe Arriba in cloud forest at 2,200 m. There is a well-defined dry season, running from December to April, at BCI, Las Cumbres and Boquete. At none of the other sites is there a dry season. At Fortuna there seems to be less rain in February-May, at both Guadalupe Arriba and Corriente Grande rainfall is bimodal with slightly less rain in February and September (Corriente Grande) or April and November (Guadalupe Arriba) and at Miramar there is no indication of any seasonality in rainfall at all. For further details about these sites see Wolda et al. (1996).

The insect groups used here are a number of groups of Coleoptera, mostly families, such as Pselaphidae (see Wolda & Chandler, 1996) Curculionoidea (see Wolda et al., 1996), Cerambycidae, Chrysomelidae, Scarabaeidae, and other Coleoptera. Plus Homoptera, Blattaria (Wolda, 1983; Wolda et al., 1983), Dermaptera (Brindle, 1988), Pentatomidae, Orthoptera and Sphingidae.

The only data that do not cover at least one year are those from Corriente Grande where the light-trap was operated during only four months. All other data are for at least one year but often cover longer periods, up to 20 years (Homoptera from BCI). The actual length of the series depends both on the site and on the taxa. Weevils (Curculionoidea), Blattaria, and Homoptera are the only taxa analysed at all seven sites, but at Guadalupe Arriba only two species of Blattaria were found and those only occasionally, so that in the analysis this information had to be ignored. The other taxa either did not occur at all or were not represented in all sites.

Data analysis

Comparisons of different insect samples, taking into account presence as well as relative abundance of the species concerned, have often been made, but usually using inadequate techniques.

The only similarity index suitable for this analysis, one that ranges in value from zero (samples do not have any species in common) to one (samples are random samples from the same fauna), one that is not too biased towards the effects of the more common species, and one that has an estimate of the variance so that statistical tests can be performed, is the NESS-similarity index (GRASSLE & SMITH, 1976; SMITH et al., 1979). Unfortunately, a computer program is needed to do the calculations. For the 'm'-parameter a value of 20 was chosen whenever possible.

The temperate data

There are a large number of publications on samples of weevils (Curculionoidea) from southern Poland. The samples are taken in a large variety of biotopes and at all sorts of altitudes. For references to these publications see WOLDA et al. (1996).

MORIMOTO & MIYAKAWA (1985) present data on weevils (Curculionoidea) from nine of the Izu islands in Japan.

RAATIKAINEN & IIVARINEN (1986) studied the beetle fauna in 54 hay meadows all over Finland. The samples cover a very large area, but are taken in very similar habitats. In WOLDA et al. (1996) only the data on weevils were reported, while here all beetles are included.

RAATIKAINEN & HUHTA (1968) present data on the spider fauna in twelve oat fields distributed in the Southern half of Finland.

Moths were studied by means of light-traps at three sites in the Czech Republic, one in urban Brno, one in a wetland forest at Černiš in Southern Bohemia and one in a deteriorated agricultural setting near České Budějovice (cf. WOLDA et al., 1994).

Moths were also collected by light-traps at four sites in Kansas and two sites in Nebraska, USA (WALKDEN, 1942). The sites vary in altitude between 270 and 1,300 m.

Extensive data sets on butterflies are available from natural habitats in the British Isles (POLLARD et al., 1986). Only the data from 36 of the sites with the longest series are used here.

Ground beetles (Carabidae) were collected by pitfall-traps in NE Netherlands over many years in a variety of habitats (DEN BOER, 1977 and pers. comm.). Data are used here from 28 sites.

At 15 sites in the foothills of the Harz mountains in Germany carabids were collected by STUBBE (1982).

These samples of Carabidae from the Netherlands were combined in one large sample as were those from the Harz, and these were compared with other samples from Western Europe such as Saarbrücken (KLOMANN, 1977), several forests in Southern Belgium (BAGUETTE, 1987), one site in extreme South Belgium (LEBRUN et al., 1987) and in a series of Belgian peat bogs (DUFRÊNE, 1987).

Homoptera were sampled in a large variety of biotopes in Northern Karelia, Finland, by KONTKANEN (1950). Only the data from his table 26 with 30 biotopes sampled at roughly the same time are used here.

Four different meadows in Poland were sampled by ANDRZEJEWSKA (1965) for Homoptera with three different techniques. The results from the techniques are combined here for each meadow.

Data on Homoptera from 28 different oat fields scattered all over Southern Finland are given by RAATIKAINEN & VASARAINEN (1976).

In Finnish Lapland and Norwegian Finmark Homoptera were sampled at a large number of sites with habitats ranging from forests to old fields to grasslands (RAATIKAINEN & YLÖNEN, 1988). Samples with very few (<10) species were ignored here so that 17 samples are available for analysis.

LINNAVUORI (1952) sampled Homoptera in a series of different biotopes in Southwestern Finland.

EMMRICH (1966) gives data on Homoptera from 17 sites in Mecklenburg, Northern Germany. The sites are grasslands or agricultural fields.

ŁOMNICKI (1963) studied arthropods at a large number of sites the Tatra mountains of Southern Poland. He combined the results in three habitat types.

Data on chironomid midges from five sites along the Schill River in Rumania are available through the work of CURE & POPESCU-MARINESCU (1977).

DARSIE et al. (1953) present data on two large mosquitoes samples, covering 20 years, taken at two sites in Delaware, USA.

Results

Panamanian Tropics

A list of all available NESS-similarity indices for the 12 insect groups and seven localities is given in table 1.

Similarity values range from zero to 0.741, with an average of 0.170. Only six out of the 153 values in table 1 are over 0.5 and only 14 are over 0.4. Sixty nine values are under 0.1 and 20 values are even under 0.01.

In all of the comparisons the similarity values were significantly different from unity, i.e. no two samples were sufficiently alike to be considered samples from the same fauna.

The standard deviations of the indices are not included, but they are generally low to very low, averaging 0.014. It is useful to compare between-year similarities from the same site. These comparisons yielded 65 between-year similarity-indices with a mean of 0.822, ranging from 0.472 to 0.976, which were almost all significantly different from unity, showing that real changes in the fauna do occur between-years. Between-years values are much higher than between-site values, indicating that between-year similarities at any one site are much larger than between-site similarities.

A closer look at the Homoptera illustrates the meaning of the rather abstract similarity values of table 1. Of the total 2,160 species almost two thirds (1,388 species, 64.3%) were found at only one site and another quarter (504 species, 23.3%) at only two sites. Only 32 species (1.5%) were found at five or more of the seven localities.

The indices in table 1 are not just a random set of values. There is a definite pattern. All similarity-values for the BCI-Las Cumbres comparisons are high, Miramar scores fairly high versus both BCI and Las Cumbres while Corriente Grande has somewhat lower values as compared to these other three lowland sites. The mountain sites are very different from the lowland sites and also differ among themselves. Boquete and Fortuna are only 20 km from each other, but the similarity indices vary from zero to 0.37, undoubtedly due to the fact that these sites are in very different habitats and climate. Some data are not included in table 1, such as Psocoptera (BROADHEAD & WOLDA, 1985) for which only BCI and Fortuna data are available. The NESS-value here is 0.078 ± 0.004, which fits in right in the middle of the other points for the BCI-Fortuna comparison in table 1.

This pattern can be best expressed by a between-group correlation matrix for similarity values, which is given in table 2. Only correlations based on at least six pairs of similarity-indices are included. All correlations are positive, with an average of 0.675 and a standard deviation of 0.174. Of the 57 correlation coefficients, 44 are larger than 0.6 and 14 are larger than 0.8. Only two correlations are smaller than 0.3, i.e. Pselaphidae vs Chrysomelidae (0.298) and Dermaptera vs Chrysomelidae (0.179).

Table 1. NESS-Similarity indices between each pair of seven sites in Panama for 12 groups of insects: BCI. Barro Colorado Island; LC. Las Cumbres; Mir. Miramar; C.Gr. Corriente Grande; Boq. Boquete; For. Fortuna; Gua. Guadalupe Arriba. P. Pselaphidae; Cu. Curculionoidea; Bl. Blattaria; D. Dermaptera; H. Homoptera; C. Cerambycidae; Ch. Chrysomelidae; Sc. Sacarabaeidae; o-Co. "other" Coleoptera; Pe. Pentatomidae; O. Orthoptera; S. Sphingidae.

Índices de similaridad de NESS entre cada par de las siete zonas estudiadas en Panamá paras cada uno de los 12 grupos de insectos. (Para las abreviaturas, ver arriba).

	Groups of insects											
	P	Cu	Bl	D	H	C	Ch	Sc	o-Co	Pe	O	S
BCI vs LC	0.648	0.378	0.741		0.427					0.466	0.568	0.587
BCI vs Mir	0.159	0.469	0.399	0.614	0.381	0.282	0.141	0.259	0.264	0.235	0.579	
BCI vs C.Gr.	0.219	0.281	0.289	0.440	0.359					0.093		
BCI vs Boq	0,000	0.148	0.228	0.169	0.162	0.028	0.108	0.217	0.027	0.061	0.276	
BCI vs Fort	0.002	0.168	0.006	0.000	0.051	0.094	0.067	0.106	0.041	0.051	0.100	0.293
BCI vs Gua		0.035			0.078	0.000	0.000	0.000	0.035			0.081
LC vs Mir	0.230	0.384	0.352		0.444					0.212	0.461	
LC vs C.Gr.	0.299	0.236	0.291		0.274					0.014		
LC vs Boq	0.000	0.172	0.247		0.171					0.041	0.389	
LC vs Fort.	0.002	0.116	0.057		0.037					0.067	0.082	0.252
LC vs Gua		0.027			0.063							0.058
Mir. vs C.Gr.	0.354	0.359	0.427	0.577	0.294					0.041		
Mir. vs Boq	0.000	0.161	0.212	0.228	0.196	0.073	0.226	0.014	0.058	0.151	0.341	
Mir. vs Fort.	0.012	0.194	0.052	0.011	0.036	0.067	0.065	0.016	0.127	0.010	0.264	
Mir. vs Gua.		0.038			0.063	0.000	0.000	0.000	0.070			
C.Gr. vs Boq	0.007	0.152	0.082	0.224	0.105					0.030		
C.Gr. vs Fort.	0.114	0.246	0.099	0.315	0.071					0.000		
C.Gr. vs Gua.		0.026			0.043							
Boq. vs Fort.	0.093	0.240	0.370	0.000	0.258	0.273	0.224	0.183	0.250	0.144	0.276	
Boq. vs Gua.		0.009			0.152	0.007	0.012	0.028	0.115			
For. vs Gua.		0.058			0.011	0.000	0.003	0.073	0.155			0.011

Table 2. Between-group correlations in between-site NESS-Similarity indices. The number of indices available for each group are also given. Only correlations based on at least six NESS pairs were included. All correlations are positive and the vast majority is significantly to highly significantly different from zero. (For abbreviations see table 1).

Índices de similaridad de NESS. También se da el número de índices disponible para cada grupo. Sólo se incluyen las correlaciones basadas al menos en seis pares de NESS. Todas las corrrelaciones son positivas y la gran mayoría son significativamente diferentes de cero. (Para las abreviaturas ver tabla 1).

	Indices										
	21	15	10	21	10	10	10	10	15	10	6
	Cu	Bl	D	H	C	Ch	Sc	o-Co	Pe	Or	S
P	0.705	0.858	0.768	0.735	0.940	0.298	0.673	0.929	0.664	0.677	
Cu	-	0.734	0.796	0.827	0.885	0.626	0.747	0.653	0.608	0.846	0.972
Bl		-	0.630	0.867	0.749	0.685	0.686	0.721	0.803	0.831	
D			-	0.714	0.423	0.179	0.514	0.404	0.327	0.915	
H				-	0.801	0.688	0.694	0.614	0.702	0.880	0.849
C					-	0.712	0.713	0.792	0.757	0.556	
C						-	0.477	0.368	0.658	0.350	
S							-	0.519	0.507	0.452	
o-Co								-	0.649	0.632	
Pe									-	0.744	
O										-	
S											-

The Temperate Zone

For a variety of temperate zone data, the average between-site similarity values plus their ranges are presented in table 3. For each data set there is a large variation in NESS-values and the averages range from 0.143 to 0.865. Some sets cover a great variety of habitats and/or altitudes and these include the data on Curculionoidea in Southern Poland, moths in the Czech Republic, butterflies in Britain, Carabidae in Western Europe and Homoptera in Northern Finland and Norway. For these data, the mean similarity index tends to be near 0.25 to 0.30 with the exception of the British butterflies where a much higher average between-site similarity was found (0.634).

Some data sets cover a large area but the samples were taken in just one kind of habitat such as the spiders and Homoptera in Finnish oat fields, beetles in Finnish hay meadows and Homoptera in Kansas and Nebraska. For these four sets, the average mean NESS value is 0.672, with a range from 0.516 to 0.800. The other data sets tend to cover much smaller areas, either covering similar habitats (Homoptera in Poland, Mosquitos in Delaware, Chironomidae in Rumania, mean similarity 0.621) or including diverse habi-

Table 3. Between-site NESS-similarity indices, mean and range, for a variety of temperate zone insect groups and sites. The Panama data are included for comparison. For sources of the data see Methods section of text.

Índices de similaridad de NESS entre zonas, media y variación, para varios grupos de insectos de zonas templadas pertenecientes a distintas áreas. Se incluyen en la comparación los datos de Panamá. Para la procedencia de los datos, ver Métodos.

Area	Group	Mean NESS	Range NESS
S Poland	Curculionoidea	0.303	0.101-0.756
Japan, Izu Islands	Curculionoidea	0.505	0.305-0.727
Finland, hay meadows	Coleoptera	0.516	0.020-0.961
NE Netherlands	Carabidae	0.370	0.017-1.002
Germany, Harz	Carabidae	0.865	0.460-0.992
Germany/Belgium/Netherlands	Carabidae	0.291	0.075-0.510
S Finland, oats	Spiders	0.800	0.469-1.089
Czech Republic	Lepidoptera	0.282	0.166-0.465
Kansas/Nebraska, USA	Lepidoptera	0.619	0.362-0.921
Britain	Butterflies	0.634	0.168-0.933
N Karelia, Finland	Homoptera	0.345	0.000-0.954
Poland	Homoptera	0.502	0.104-0.932
S Finland, oats	Homoptera	0.753	0.399-0.989
SW Finland	Homoptera	0.143	0.000-0.604
N Finland, N Norway	Homoptera	0.248	0.000-0.804
Germany, Mecklenburg	Homoptera	0.304	0.000-0.912
Delaware, USA	Mosquitos	0.733	---
Rumania, Schill-watershed	Chironomidae	0.629	0.506-0.706
S Poland	Invertebrates	0.711	0.707-0.715
Panama	Various	0.170	0.000-0.741

tats within a relatively small geographic region such as Carabidae in NE Netherlands, Homoptera in N Karelia, Homoptera in SW Finland and Homoptera in N Germany. For these, the average mean NESS is 0.291, ranging from 0.143 to 0.370. The high average similarity value of 0.711 for invertebrates from the high Tatras in Southern Poland may show that the habitats selected were not very different, or that for the invertebrates concerned, between-site similarities tend to be higher than for other groups. One anomaly here is formed by the weevils from the Izu Islands in Japan, where the moderately large average NESS of 0.505 does not correspond to the large areas covered by these nine islands and the statement by the authors that 'their biota is greatly different according to the geologic and volcanic history'.

Not surprisingly, different habitats have faunas that differ greatly from each other, especially if they cover a larger geographic area, than are faunas from similar habitats even if they do cover a large area.

Discussion

Species in tropical sites not only vary in richness, but also in composition. Between-site similarities tend to be low to very low. The highest similarities were found between the four lowland sites, especially between Barro Colorado Island and Las Cumbres, two sites in or near the Panama Canal area, and only 40 km apart, but very different in habitat. BCI is a well-preserved tropical forest and Las Cumbres is a residential area with some young second growth forest. BCI is situated towards the more humid Atlantic side of the isthmus of Panama while Las Cumbres is on the drier Pacific side. Nevertheless, the overlap in fauna between these two sites, although far from complete, is notable. The other two lowland sites that have also some moderate similarity with BCI and Las Cumbres are Miramar and Corriente Grande, both in North-west Panama, and without a dry season. Miramar is at a coastal pasture at the bottom of a very impoverished forested slope and Corriente Grande is in good old forest that was only recently selectively logged. Moderate similarity values were found in spite of the extreme differences in habitat. On the other hand, similarities between these lowland sites and the mountain sites are low to very low, which shows that at moderate (1,000-1,300 m) and higher (2,200 m) altitudes faunas are completely different from those in the lowlands. Large differences are seen even among the montane sites. Some moderate similarity values are observed only for the Boquete-Fortuna comparison, two sites that are only 20 km apart, although the habitat and climate are very different. Strong effects of altitude were also found in the temperate zone (Luff & Woiwod, 1995).

The similarity indices were calculated for all available data in twelve different insect groups, varying from earwigs to Homoptera and from weevils to cockroaches. The between-site comparisons are very similar in all groups. If a site A is very different from site B in group X, then these two sites also tend to be very different in the other groups and if two sites are moderately similar in species composition in group Y, they also tend to be moderately similar in the other groups. If this conclusion holds up for other data, it means that in order to evaluate differences in fauna between two sites, an analysis of the complete fauna is not necessary, and that an analysis of one or two groups would suffice. There are few other tropical data that could be used here in comparison. Data on Panamanian horse-flies, Tabanidae (Fairchild, 1942 and pers. comm.) show an average similarity-value for a comparison between several sites in the Panama Canal area, both on the Atlantic and the Pacific side, of 0.583 (ranging from 0.176-0.960), roughly comparable to the present BCI-Las Cumbres comparison, and the average similarity between these sites and Almirante (near Miramar) is 0.143 (0.01-0.357). These values also fit in well with the present data (table 1).

How do these between-site comparisons in the tropics compare with such comparisons in the temperate zone? This cannot be answered as yet with any degree of certainty. Between-site similarities in faunal composition depend on similarities in habitat and on geographic distances between the sites. For an exact tropics-temperate zone comparison of faunal similarities, habitats would have to be carefully selected in both regions so that they could be matched in between-site differences in environment. This has not been done and it may not even be possible, considering the major differences in climate. For example, are the between-site differences in habitat at the weevil sites in southern Poland larger or smaller than the between-site differences in Panama? What we are dealing with is a number of data from the temperate zone, and some Panamanian data, all summarized in table 3, which show a large range of similarity values for each and every set of data with a wide overlap between data sets. The averages for all but one of the temperate data sets, however, even for that from a large geographic area with a wide variety of habitats, are larger or much larger than the average for Panama, in spite of the fact that the area covered by the Panamanian samples is much smaller than that of many of the temperate areas listed. This emphasizes the large between-site diversity in the tropics, at least in Panama, and suggests that this diversity may be larger than is usually observed in the temperate zone. However, the analysis of other tropical data sets does not appear to support this trend.

Trapido et al. (1955) and Trapido & Galindo (1957) present extensive data on mosquitoes in the Pacific lowlands of Panama, two sites in the mountains (perhaps comparable to Boquete), and at Almirante in NW-Panama, near Miramar. The between-site similarities for these mosquitoes are an average of 0.374 (0.241-0.679) between the Canal area and the mountains, 0.668 (0.596-0.770) between the Canal area and Almirante and 0.605 (0.536-0.696) between the mountains and Almirante. These values are very high compared with those for the other insect groups. Grjebine et al. (1977) studied mosquitoes in the Congo Republic and for their three sites the average between-site similarity index is also high, viz. 0.746 (0.645-0.816). It is unclear how far apart these sites are or how different the environments are, but the similarities are very high compared with all the others discussed in the present paper. It seems that similarity values for mosquitoes, if used for between-site faunal comparisons, would overestimate those for other insects. It is interesting that the similarity between two Delaware sites in mosquito faunas is also high (table 3).

Faunas of fruit flies (Drosophilidae) also in the tropics seem to have between-site similarities that are much larger than those reported in this paper, and similar to those found for mosquitoes. A set of 45 *Drosophila* samples, collected over a very large area of Brazil (Sene et al., 1980) and in a great variety of habitats, has an average between-site similarity of 0.499 (0- 0.980) and data on nine sites from a large area in SW India covering a variety of habitats (Prakash & Reddy, 1984; Reddy & Kishnamurthy, 1976-77), produce an average between-site similarity-value of 0.597 (0.375-0.856).

A set of data from different habitats at the Kibale forest in Uganda (Nummelin & Hanski, 1989) shows large between-site similarities in dung beetle faunas.

Although the present data suggest that between-site similarities in the faunal composition of several insect groups in the tropics are larger than those found in temperate areas, some data from the literature are not in agreement. The inevitable conclusion seems to be that there are sometimes large between-site differences in faunal composition, both in the temperate zone and in the tropics, that such differences may in certain cases depend on the group of insects one is dealing with or with the area of study, but that clear-cut tropical-temperate differences may not occur.

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Resumen

Similaridades entre faunas en la composición de especies de varios grupos de insectos de Panamá

Se estudiaron las similitudes en la composición faunística de siete localidades de la República de Panamá utilizando 12 grupos de insectos tropicales recolectados con trampas de luz. Se compararon los resultados con algunos datos encontrados en la literatura tanto referentes a la zona templada como al trópico.

Existen grandes diferencias entre las faunas analizadas, especialmente en relación a la altura. Las diferencias entre las localidades fueron muy similares en los grupos estudiados.

Esto sugiere pues que no es necesario estudiar muchos grupos de insectos para comparar la similaridad faunística de varios lugares, bastando con uno o dos grupos.

Hay que ser cauteloso al comparar la zona templada con el trópico. De todos modos la información disponible sugiere que mientras que las diferencias entre localidades panameñas tienden a ser más grande que entre las de la zona templada, los datos de la literatura muestran que esto no es necesariamente una tendencia general.

References

ANDRZEJEWSKA, L., 1965. Stratification and its dynamics in meadow communities of Auchenorrhyncha (Homoptera). *Ekologia Polska*, A,13: 685-715.

BAGUETTE, M., 1987. Spring distribution of carabid beetles in different plant communities of Belgian forests. *Acta Phytopath. Entomol. Hung.*, 22: 57-69.

BRINDLE, A., 1988. Dermaptera at light in Panama. *Entomol. Mo. Mag.*, 124: 45-56.

BROADHEAD, E. & WOLDA, H., 1985. The diversity of Psocoptera in two tropical forests in Panama. *J. Anim. Ecol.*, 54: 739-754.

CURE, V., & POPESCU-MARINESCU, V., 1977. Ein Beitrag zur Kenntnis der Chironomiden-populationen (Diptera) des Schill-(Jiu-) Beckens (Rumänien). In: *Verh. VI Intern. Symp. Entomofaunistik Mitteleuropa*: 125-135 (H. Malicky, Ed.). Junk, Den Haag, The Netherlands.

DARSIE JR., R. F., MACCREARY, D., & STEARN, L. A., 1953. Analysis of mosquito-trap collections at Delaware City and Lewes, Delaware, for the twenty-year period, 1932-1951. *Proc. 40 Ann. Meet., N. J. Mosquito Exterm. Assoc.*: 169-190.

DEN BOER, P. J., 1977. *Dispersal power and survival. Carabids in a cultivated countryside*. Veenman, Wageningen, The Netherlands.

DUFRÊNE, M., 1987. Distribution of carabid beetles in a Belgian peat bog: Preliminary results. *Acta Phytopath. Entomol. Hung.*, 22: 349-355.

EMMRICH, R., 1966. Faunistisch-Ökologische Untersuchungen über die Zikadenfauna (Homoptera Auchenorrhyncha) von Grünlandflächen und Landwirtschaftlichen Kulturen des Greifswalder Gebietes. *Mitt. Zool. Mus. Berlin*, 42: 61-126.

FAIRCHILD, G. B., 1942. The seasonal distribution of some Tabanidae (Dipt.) In Panama. *Ann. Entomol. Soc. Am.*, 35: 85-91.

GAULD, I. D., 1987. The so-called «anomalous diversity» of tropical Ichneumonidae re-examined. *Biol. J. Linn. Soc.*, 30: 299-312.

GRASSLE, J. F. & SMITH, W., 1976. A similarity measure sensitive to the contribution of rare species and its use in investigation of variation in marine benthic communities. *Oecologia*, 25: 13-22.

GRJEBINE, A., GRILLOT, J.-P. & LAURENTIN, M.-F., 1977. Moustiques de l'île M'Bamou (Congo). II. Quelques espèces aggressives de Culicidae (Diptera) de la région du Stanley-Pool. *Bull. Mus. Hist. Nat.*, 3e sér. num. 483, Écol. Génér., 40: 201-236.

JANZEN, D. H., 1981. The peak in North American Ichneumonid species richness lies between 38° and 42° N. *Ecology*, 62: 532-537.

KLOMANN, U., 1977. Bodenarthropoden als Belastungsindikatoren in urbanen Räumen. In: *Verh. VI Intern. Symp. Entomofaunistik Mitteleuropa*: 221-232 (H. Malicky, Ed.). Junk, Den Haag, The Netherlands.

KONTKANEN, P., 1950. Quantitative and

seasonal studies on the leafhopper fauna of the field stratum on open areas in North Karelia. *Ann. Zool. Soc. Bot. Fenn. 'Vanamo'*, 13:1-91.

LEBRUN, PH., BAGUETTE, M., & DUFRÊNE, M., 1987. Species diversity in a carabid community: comparison of values estimated at 23 years. *Acta Phytopath. Entomol. Hung.*, 22: 165-173.

LINNAVUORI, R., 1952. Studies on the ecology and phenology of the leafhoppers (Homoptera) of Raisio (SW Finland). *Ann. Zool. Soc. Zool. Bot. Fenn. 'Vanamo'*, 14: 1-32.

ŁOMNICKI, A., 1963. The distribution and abundance of ground-surface-inhabiting arthropods above the timber line in the region of Zólta Turnia in the Tatra Mountains. *Acta Zool. Cracov.*, 8: 183-249.

LUFF, M. L. & WOIWOD, I. P., 1995. Insects as indicators of land-use change: a European perspective, focussing on moths and ground beetles. In: *Insects in a changing environment*: 399-422 (R. Harrington & N. E. Stork, Eds.). Academic Press, London.

MICHENER, C. D., 1979. Biogeography of the bees. *Ann. Miss. Botan. Garden*, 66: 277-347.

MORIMOTO, K. & MIYAKAWA, S., 1985. Weevil fauna of the Izu Islands, Japan (Coleoptera). *Mushi*, 50: 19-85.

NUMMELIN, M., & HANSKI, I., 1989. Dung beetles of the Kibale Forest, Uganda; comparison between virgin and managed forests. *J. Trop. Ecol.*, 5: 349-352.

OWEN, D. F., 1974. Species diversity in temperate and tropical Ichneumonidae. *Nature*, 249: 583-584.

POLLARD, E, HALL, M. L., & BIBBY, T. J., 1986. *Monitoring the abundance of butterflies*. Nature Conservancy Council, Peterborough, U. K.

PRAKASH, H. S., & REDDY, G. S., 1984. Distribution of *Drosophila* species and their diversities in the tropical rain forests of Western Ghats. *J. Bombay Nat. Hist. Soc.*, 81: 323-345.

RAATIKAINEN, M., & HUHTA, V., 1968. On the spider fauna of Finnish oat fields. *Ann. Zool. Fenn.*, 5: 254-261.

RAATIKAINEN, M. & IIVARINEN, R., 1986. Beetle fauna of field layer in hay meadows in Finland. *Acta Entomol. Fenn.*, 46: 1-42.

RAATIKAINEN, M., & VASARAINEN, A., 1976. Composition, zonation and origin of the leafhopper fauna of oatfields in Finland. *Ann. Zool. Fenn.*, 13: 1-24.

RAATIKAINEN, M., & YLÖNEN, H., 1988. Zikadenfauna verschiedener Biotope Nordfinnlands und Nordnorwegens. *Ann. Entomol. Fenn.*, 54: 73-88.

REDDY, G. S. & KRISHNAMURTHY, N. B., 1976-77. Temporal changes in the population densities of different species of *Drosophila*. *J. Mysore University*, B, 27: 113-137.

SENE, F. M., VAL, F. C., VILELA, C. R., & PEREIRA, M. A. Q. R., 1980. Preliminary data on the geographical distribution of *Drosophila* species within morphoclimatic domains of Brazil. *Papéis Avulsos Zool., S. Paolo*, 33: 315-326.

SMITH, W., KRAVITZ, D. & GRASSLE, J. F., 1979. Confidence intervals for similarity measures using the two-sample jackknife. In: *Multivariate methods in ecological work:* 253-262 (J. F. Grassle, G. P. Patil, W. Smith & C. Taillie, Eds.). Inter Coop. Publ. House, Fairland, Maryland, USA.

STUBBE, A., 1982. Untersuchungen zur Ökologie der Carabidenfauna (Insecta, Coleoptera) des Hakelwaldes im Nordharzvorland. *Hercynia, N.F. (Leipzig)*, 19: 42-73.

TRAPIDO, H., & GALINDO, P., 1957. Mosquitos associated with sylvan yellow fever near Almirante, Panama. *Am. J. Trop. Med. Hyg.*, 6: 114-144.

TRAPIDO, H., & GALINDO, P., & CARPENTER, S. J., 1955. A survey of forest mosquitos in relation to sylvan yellow fever in the Panamanian Isthmian area. *Am. J. Trop. Med. Hyg.*, 4: 525-542.

WALKDEN, H. H., 1942. *Owlet moths (Phalaenidae) taken at light traps in Kansas and Nebraska*. Circular No. 643. U.S. Dept. Agric., Washington, D.C.

WOLDA, H., 1983. Diversity, diversity indices and tropical cockroaches. *Oecologia,* 58: 290-298.
- 1987. Altitude, habitat, and tropical insect diversity. *Biol. J. Linn. Soc.*, 30: 313-323.
WOLDA, H.. & CHANDLER, D., (in press). Diversity and seasonality of tropical Pselaphidae and Anthicidae (Coleoptera). *Proc. Kon. Ned. Acad. Wetensch. C.*
WOLDA, H., FISK, F. W. & ESTRIBÍ, M., 1983. Faunistics of Panamanian Cockroaches. *Uttar Pradesh J. Zool.*, 9: 1-9.
WOLDA, H., MAREK, J., SPITZER, K., & NOVAK, I., 1994. Diversity and variability of Lepidoptera populations in urban Brno, Czech Republic. *Eur. J. Entomol.*, 91: 213-226.
WOLDA, H., O'BRIEN, C. W. & STOCKWELL, H. P., (in press). Weevil diversity and seasonality in tropical Panama as deduced from light-trap catches (Coleoptera: Curculionoidea). *Smithson. Contr. Zool.*