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INSECT SPECIES DIVERSITY IN THE TROPICS : SAMPLING METHODS AND A CASE STUDY[1]

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(With ten text-figures)

The tropical regions of the world generally have a richer store of biological diversity than other regions of the globe. But most tropical habitats face a significant threat of destruction. Yet, little is known about tropical biotic communities. Suspecting that at least part of the reason for the poor documentation of tropical insect communities is the lack of appropriate research methodology, we have endeavoured to standardize a package of methods for quantitative sampling of insects, suitable for tropical ecologists with modest research budgets. This methodology includes the use of a small light trap as well as net sweeps, pitfall traps and scented traps. The methods have been used to sample insect species diversity patterns in three replicate one hectare plots each in twelve selected sites in the Uttara Kannada district of Karnataka, India. During this case study, we have encountered 16,852 adult individuals belonging to 1,789 species, 219 families and 19 orders of insects. Here, we provide evidence that this methodology is adequate for sampling insects and differentiating habitats on the basis of the distribution of insect species. Some interesting biological problems that tropical ecologists can study with the data generated from the application of these methods are also briefly illustrated.

INTRODUCTION

One of the few relatively undisputed generalizations in community ecology is a latitudinal gradient of increase in biological species richness and diversity from the temperate regions to the tropics (see Krebs 1985, Colinvaux 1986). Apart from being something of a rule in community ecology this means that those of us who live in the tropics enjoy a biologically rich environment. Recent work suggests that the richness of the tropical insect fauna is beyond all earlier expectations (Erwin and Scott 1980, Erwin 1983 and Stork 1988). It is equally undisputed, however, that most tropical organisms are poorly studied and the little that we do know about any group of organisms comes largely from studies of temperate species. This is expressed most dramatically in the statement that the number of biologists is negatively correlated with the number of biological species in different regions of the globe (Robinson 1978). The poor state of our understanding of tropical biology may be partly attributed to the relative economic backwardness of tropical countries, the lack of facilities for research and sometimes to the lack of the tradition of modern scientific work.

We suggest, however, that at least sometimes this is due to the lack of appropriate research methodology suitable for tropical conditions. Studies on insect species diversity and the long term monitoring of insect species and populations in different habitats are good examples. Almost all the major long term insect monitoring programmes are based on light trap catches, a method that requires uninterrupted supply of electricity, often in the mid-

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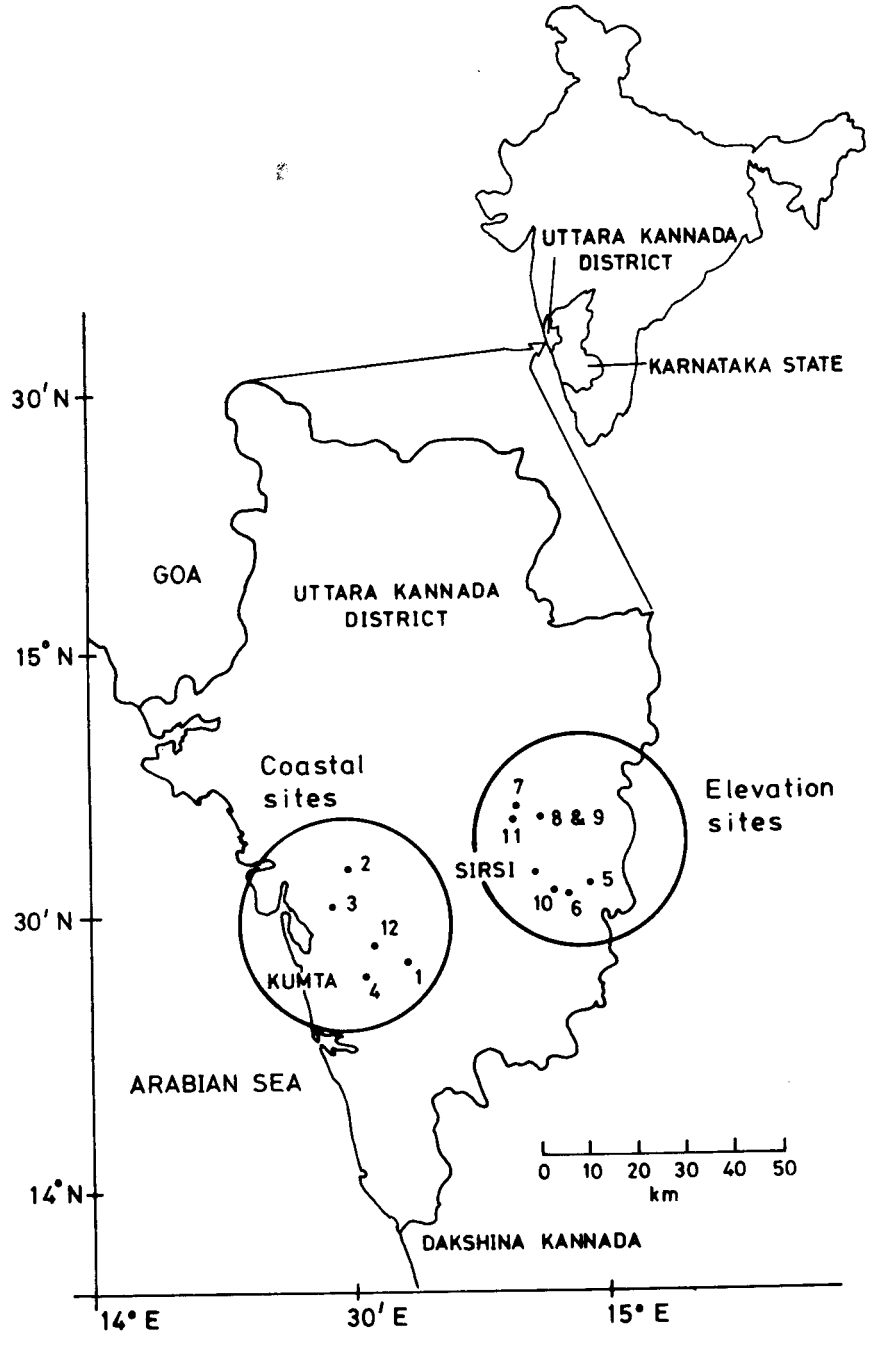

Fig.1. Map of Uttara Kannada district showing the 12 sites used in the study.
1. Santagal R.F., 2. Nagur R.F., 3. Mirjan M.F., 4. Chandavar M.F., 5. Bengle M.F., 6. Bidaralli R.F., 7. Sonda R.F., 8. Bhairumbe M.F., 9. Betta land, 10. *Eucalyptus* plantation, 11. Teak plantation, 12. *Areca* plantation.

dle of a forest (Holloway 1983, 1987; Taylor 1978, Taylor *et al.* 1976, Wolda 1983a, b; Wolda and Roubik 1986). Sometimes the light traps are operated for years together without interruption. In most tropical situations, uninterrupted supply of electricity is nearly impossible even in cities and towns, let alone in the middle of a forest. The establishment and long term maintenance of electricity generating devices is prohibitively expensive for most ecologists working in tropical countries.

Suspecting that this has prevented many tropical ecologists from undertaking insect species diversity studies (see Wolda 1981a), we have attempted to standardize a package of methods for quantitative sampling of insects, suitable for tropical ecologists with modest research budgets. Our methodology is based on the use of a small light trap using routinely available dry batteries but substantially supplemented by other methods such as net sweeps, pitfall traps and scented traps. We show here that such a methodoloy is adequate for sampling insects and differentiating habitats on the basis of insect species distribution. We also briefly illustrate some interesting biological questions that ecologists in tropical countries can begin to ask with the data generated from such methodology.

Materials and Methods

Study sites: All our study sites were located in the Uttara Kannada district of the state of Karnataka, India (Fig. 1). The forested study sites fall broadly into two categories reflecting different levels of disturbance, namely, the Reserve Forests (R.F.) (relatively less disturbed) and the Minor Forests (M.F.) (relatively more disturbed). Sites representing both these categories were chosen in the coastal plains as well as at higher elevations (approximate altitude 600 m).

Selection of study sites in this manner ensured that these sites represent habitats under different environmental conditions and levels of disturbance. In addition to these forested habitats, three monoculture plantations (Pl.) and a leaf manure forest (Betta land) were also chosen for the study. At each of these sites, sampling was carried out in three one hectare plots. Thus a total of 36 one hectare plots from 12 habitat types were sampled (Table 1). A brief description of each study site is given in Table 2. All sampling was carried out during December, January, February and March which is part of the dry season in these localities.

Sampling methods: To develop a package of methods for quantitative sampling of insect species, collections were made using four different methods which were standardized after extensive field trials.

1. **Light trap:** A portable light trap which can be easily assembled and dismantled was fabricated using locally available inexpensive material. The light trap uses a fluorescent light source (Eveready Fluorolite 7.5 inch; 6 watts) powered by routinely available battery cells. The main framework of the trap consists of four iron legs, an aluminium roof and two aluminium baffles, between which the light source is placed. Insects attracted to the light were collected through a funnel in a cyanide jar, below the light. One light trap was placed in the centre of the plot. The light was switched on at dusk and allowed to burn itself out as the batteries drained after about seven hours. The insects trapped in the jar were collected the next morning and preserved in 70% alcohol.

2. **Net sweeps:** Net sweeps were carried out to collect insects off the vegetation. The nets used in systematic sweeping of the ground level vegetation were made of thick cotton cloth with a diameter of 30 cm at the mouth and a bag length of 60 cm.

For carrying out net sweeps the plot was divided into 100 quadrats, measuring 10 m x 10 m each. Six such quadrats were chosen at random and the entire ground level vegetation in the chosen quadrat was covered during the sweeping. Net sweeps were always done between 1000 h - 1200 hrs. The insects collected from each quadrat were transferred into polythene bags containing a cotton wad dipped in chloroform. Insects were later separated from the litter and preserved in vials containing 70% alcohol.

3. **Pitfall traps:** The pitfall traps consisted of a 2.5 litre plastic jar with an opening of 9 cm in diameter, buried at ground level and protected from rain by a tripod stand carrying a plastic plate of about 30 cm diameter at a distance of about 15 cm above the ground. One pitfall trap was placed in each of five randomly chosen 10 m x 10 m quadrats. Each jar carried 25 ml of 0.05% methyl parathion. The traps were set up between 1500 and 1700 hrs and were collected the next morning. Insects trapped in the jars were preserved in 70% alcohol.

TABLE 1
STUDY SITES, PLOTS AND SAMPLING PERIOD

	Reserve forest	Minor forest	Plantations	Leaf manure forest
Coastal sites	Santagal R.F. (Plot Nos. 1-3) March 1984	Chandavar M.F. (Plot Nos. 10-12) January 1984	*Areca* Pl. (Plot Nos. 34-36) January 1985	
	Nagur R.F. (Plot Nos. 4-6) February 1984	Mirjan M.F. (Plot Nos. 7-9) December 1984		
Elevation sites	Bidaralli R.F. (Plot Nos. 16-18) December 1983	Bengle M.F. (Plot Nos. 13-15) December 1983	Teak Pl. (Plot Nos. 31-33) December 1984	Betta Land (Plot Nos. 25-27) January 1985
	Sonda R.F. (Plot Nos. 19-21) December 1983	Bhairumbe M.F. (Plot Nos. 22-24) January 1984	*Eucalyptus* Pl. (Plot Nos. 28-30) December 1984	

TABLE 2
BRIEF DESCRIPTION OF STUDY SITES

Sites	Vegetation type	Dominant tree genera	Remarks
Santagal R.F.	Evergreen	*Cinnamomum, Bischofia* and *Diospyros*	Thick tree canopy, understorey of cane breaks.
Nagur R.F.	Evergreen	*Holigarna* and *Hopea*	Thick tree canopy, understorey of saplings.
Mirjan M.F.	Scrub	*Ixora, Buchanania* and *Terminalia*	Highly degraded semi-evergreen.
Chandavar M.F.	Semi-evergreen	*Ixora, Aporosa* and *Hopea*	Degraded, understorey of frequently lopped saplings.
Bengle M.F.	Moist deciduous	*Terminalia*.	*Degraded, thick undergrowth of* grass and annual herbs.
Bidaralli R.F	Moist deciduous	*Terminalia, Xylia* and *Lagerstroemia*	Undergrowth of herbs and shrubs, *mainly Clerodendrum*
Sonda R.F	Moist deciduous	*Terminalia, Xylia* and *Aporosa*	Understorey mainly of *Psychotria* spp.
Bhairumbe M.F	Moist deciduous	*Careya, Ziziphus* and *Randia*	Degraded, undergrowth of *Chromelina*.
Betta land	Moist deciduous	*Terminalia* and *Lagerstroemia*	Cleared of all undergrowth, maintained for leaf manure.
Eucalyptus Pl.	Monoculture	*Eucalyptus*	Thick undergrowth of grass and herbs, surrounded by extensive moist deciduous forest.
Teak Pl.	Monoculture	*Tectona grandis*	Little or no undergrowth except *Lantana* and *Chromelina*.
Areca Pl.	Monoculture	*Areca catechu*	Plantations in valleys, surrounded by evergreen forest on hills.

4. **Scented traps:** A plastic jar of 2.5 litre capacity was used to fabricate a scented trap. The mouth of the jar was shielded from rain water using a plastic plate allowing a gap of 6 cm between the mouth of the jar and the plastic plate so that insects could freely move into the jar. The trap was baited with 200 ml of saturated jaggery (unrefined cane sugar) solution with two tablets of baker's yeast, 0.05% (final concentration) methyl parathion and 0.5 ml of pineapple essence. The traps were hung at about 1 m from the ground on a wooden peg. Five such traps were used, one each in the centre of a randomly chosen 10 m x 10 m quadrat. The scented traps were also set between 1500 -1700 hrs and collected the following morning. Insects trapped in the jaggery solution were filtered, washed and preserved in 70% alcohol.

Thus one light trap placed in the middle of a one hectare plot working for about 7 hours (1900 to 0200 hrs), net sweeps in 6 randomly chosen 10 m x 10 m quadrats, 5 randomly placed pitfall traps and 5 randomly placed scented traps, both working for about 18 hrs each constituted one sampling unit. Each of the 36 plots were subjected to one such sampling unit.

Preservation of Specimens and Data Recording

All insects (except large moths) were stored in alcohol for future sorting. The insects were identified up to the family level and within each family, recognizable taxonomic units (RTU) were separated based on morphological differences. For convenience, the RTUs will be referred to as species throughout this paper. Each such specimen was given a serial number within that family. For each plot, site and quadrat, information on the order, family, serial number, number of nymphs or larvae and the number of adults were recorded. Only data on the adult insects are presented here.

Canopy cover index: It was obvious from our preliminary results that a subjective classification of habitats into more disturbed and less disturbed categories is insufficient to discern any relationship between patterns of diversity and levels of disturbance. An attempt was therefore made to develop an index to quantify levels of disturbance. One of the major causes of disturbance in tropical forests is a tree fall, either man made or natural, which leads to large scale changes in the understorey vegetation. The extent of canopy cover could thus be one good measure of disturbance.

A relative estimate of the extent of canopy cover was obtained by the presence or absence of canopy at randomly chosen points in the study plots. 50 such points at the corners of 10 m x 10 m quadrats were chosen to make observations on the canopy cover. At each of these points the observer counted the number of trees whose canopy intersected his line of sight immediately above his head. Shrubs, tree branches and leaves obstructing the line of sight at less than about 3 m from the ground were not counted. The number of trees which formed a canopy over these 50 points was used to obtain a mean value for the plot, which we call the Canopy Cover Index.

Data analysis:

1. **α Diversity:** Several indices of alpha (within site) diversity such as the Shannon Weiner index (Margalef 1958), Simpson's index (Simpson 1949), Hill's diversity indices N_1 and N_2 (Hill 1973, see also Gadagkar 1989), S_m (Hurlbert 1971, Wolda 1983a and α of the log series Fisher *et al.* 1943) were computed. For the sake of brevity only results using α of the log series are given in this paper. α of the log series was computed by an iterative procedure using the equation,

$$S = \alpha \log_e (1 + N/\alpha)$$

where S is the number of species in the sample, N is the number of individuals in the sample, and α is the index of diversity. The standard deviation of α was estimated as α /-log (1-X) where X = N/(N +α) (Anscombe 1950). Using this standard deviation, significant differences in diversity between habitats were judged by a z test.

2. **β Diversity:** β (between site or between method) diversity was estimated as coefficients of similarity given by the Morisita-Horn Index (after Wolda 1981b),

$$C_\lambda = \frac{2 \Sigma (n_{1i}.n_{2i})}{(\lambda_1 + \lambda_2). N_1 N_2}$$

where,

$$\lambda_j = \frac{\Sigma n^2_{ji}}{N_j^2}$$

where n_{ji} is the number of individuals of

TABLE 3
SUMMARY OF CATCH DATA

Site	Plot number	No. of orders	No. of families	No. of species	No. of individuals	Alpha of log series
Santagal R.F.	1	7	36	77	144	67.31
Santagal R.F.	2	8	33	73	231	36.77
Santagal R.F.	3	9	36	88	199	60.36
Nagur R.F.	4	10	33	59	247	24.55
Nagur R.F.	5	5	28	64	265	26.81
Nagur R.F.	6	8	30	65	213	31.88
Mirjan M.F.	7	8	40	87	950	23.31
Mirjan M.F.	8	9	48	102	874	29.93
Mirjan M.F.	9	10	44	88	1085	22.61
Chandavar M.F.	10	9	52	99	529	35.93
Chandavar M.F.	11	8	37	79	757	22.20
Chandavar M.F.	12	10	45	103	407	44.42
Bengle M.F.	13	12	77	164	496	85.58
Bengle M.F.	14	5	46	110	445	46.74
Bengle M.F.	15	10	68	171	590	80.79
Bidaralli R.F.	16	10	71	144	322	100.02
Bidaralli R.F.	17	12	67	157	539	74.44
Bidaralli R.F.	18	12	53	111	445	47.44
Sonda R.F.	19	8	35	78	204	46.15
Sonda R.F.	20	6	30	73	173	47.61
Sonda R.F.	21	4	35	67	256	29.53
Bhairumbe M.F.	22	10	30	67	175	39.69
Bhairumbe M.F.	23	9	29	58	177	30.05
Bhairumbe M.F.	24	7	43	77	301	33.44
Betta land	25	7	46	122	539	49.15
Betta land	26	10	40	100	304	51.97
Betta land	27	7	33	87	262	45.56
Eucalyptus Pl.	28	12	66	204	659	101.14
Eucalyptus Pl.	29	12	68	239	1331	84.95
Eucalyptus Pl.	30	8	52	176	1191	57.04
Teak Pl.	31	7	29	55	145	32.30
Teak Pl.	32	9	24	43	128	22.73
Teak Pl.	33	7	29	46	86	40.22
Areca Pl.	34	7	45	99	862	28.87
Areca Pl.	35	7	36	102	721	32.42
Areca Pl.	36	7	42	106	600	37.37
Total		19	219	1789	16852	506.06

species i in sample j and n_j is the number of individuals in sample j. The index was computed with data logarithmically transformed as ln $(n_{ji}+1)$. Cluster analysis was performed using a single-linkage algorithm.

RESULTS

Summary of catch data: A summary of the insect catch data in the form of the number of orders, families, species and individuals and α of the log series as an index of diversity for each of the 36 plots are shown in Table 3. In any given plot we encountered from 4-12 orders, 24-77 families, 43-239 species and 86-1331 individuals. In all the 36 plots put together we encountered 19 orders, 219 families, 1789 species and 16,852 individuals. Some patterns in this data are immediately apparent. The highest number of individuals, species and the highest diversity were seen in one or more of the *Eucalyptus* plantation plots, while the lowest number of individuals, species and the lowest diversity were seen in one or more of the teak plantation plots. Natural forest plots, including relatively less as well as the relatively more disturbed ones, were between these two extremes shown by the monoculture plantations.

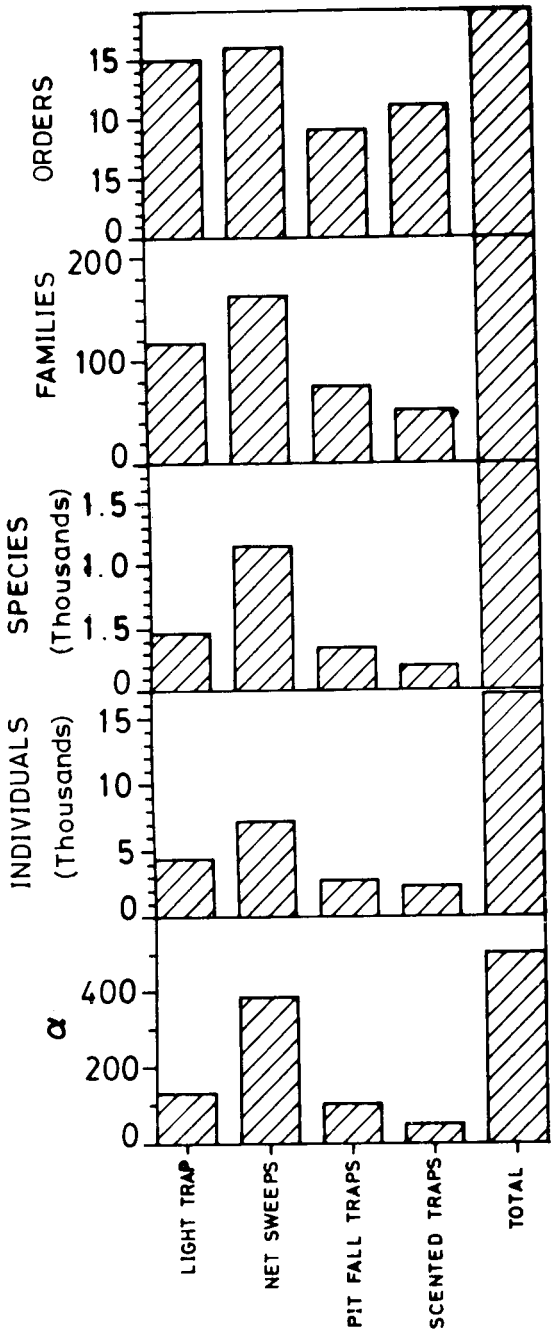

Fig.2. Numbers of orders, families, species, individuals and diversity of insects trapped by different methods.

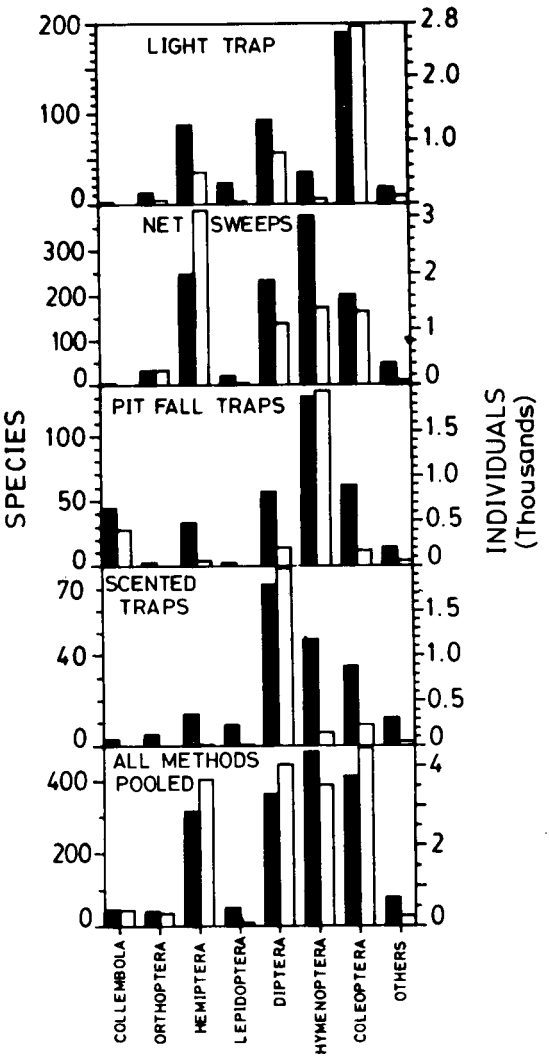

Fig.3. Taxonomic break up of insects trapped by different methods. Closed bars = species , open bars = individuals.

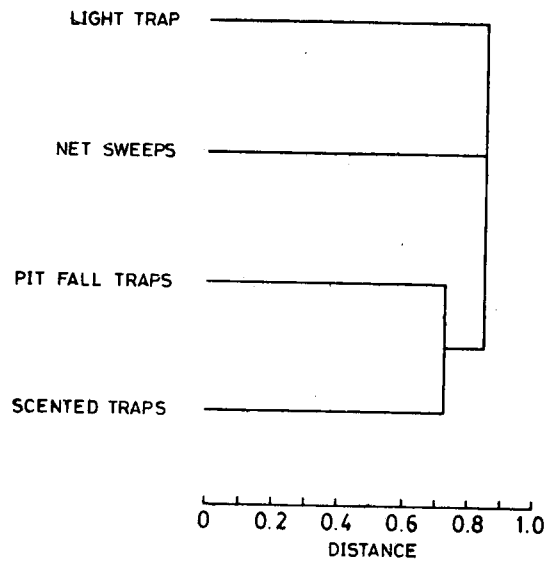

Fig.4. Dendrogram comparing insects caught by different methods (Distance = 1 – Morisita-Horn Index of Similarity). Data pooled from 36 plots.

Comparison of methods of collection: Net sweeps yielded not only the maximum numbers of orders, families, species and individuals but also the highest diversity of insects. But the remaining three methods, namely, the light trap, pitfall traps and scented traps together accounted for at least 50% of the catch (Fig. 2). The light trap yielded more Coleopterans than any other method. Most of the Hemipterans caught were in the net sweeps although net sweeps yielded an equally rich collection of Hymenopterans and Dipterans. Pitfall traps yielded more Hymenopterans than any other order while scented traps caught more Dipterans (Fig. 3).

Comparison of different species and their abundance among catches by different methods using the Morisita-Horn Diversity Index shows that each method yielded quite a different sample of insects. The similarity coefficient between any two methods ranges between 0.13 and 0.28. The consequent large distance (defined as 1 – coefficient of similarity) between insect samples obtained by different methods are shown in Fig. 4.

Since one light trap, 6 net sweeps, 5 pitfall traps and 5 scented traps were employed in each plot, we can compare the catches between different replicates of the same method. Employing the Morisita-Horn Similarity Index, we find that catches from different replicates of the same methods were by and large more similar than catches by different methods. It is important to note, however, that there

TABLE 4
COMPARISON OF DIVERSITY IN DIFFERENT CAPTURE SITES

Pairs of sites that are significantly different from each other in their levels of insect diversity as measured by α of the log series. A '+' in any cell indicates that the site mentioned in the row is significantly more diverse than the site mentioned in the column ($p < 0.05$). Numerals (1) to (12) in row and column headings refer to different sites. The mean and standard deviation of α for each site are given in the row titles. Names of sites in row titles and column titles are ordered according to diversity.

		(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1)	Bidaralli R.F. 142.89 ± 7.851				+	+	+	+	+	+	+	+	+
(2)	*Eucalyptus* Pl. 140.32 ± 6.66				+	+	+	+	+	+	+	+	+
(3)	Bengle M.F. 136.10 ± 7.37				+	+	+	+	+	+	+	+	+
(4)	Santagal R.F. 106.97 ± 7.60							+	+	+	+	+	+
(5)	Betta Land 97.53 ± 6.23							+	+	+	+	+	+
(6)	Sonda R.F. 87.93 ± 6.46									+	+	+	+
(7)	Bhairumbe M.F. 76.12 ± 5.80											+	+
(8)	Chandavar M.F. 74.09 ± 4.83											+	+
(9)	*Areca* Pl. 69.60 ± 4.47												+
(10)	Teak Pl. 60.36 ± 5.58												
(11)	Nagur R.F. 58.03 ± 4.72												
(12)	Mirjan M.F. 53.91 ± 3.67												

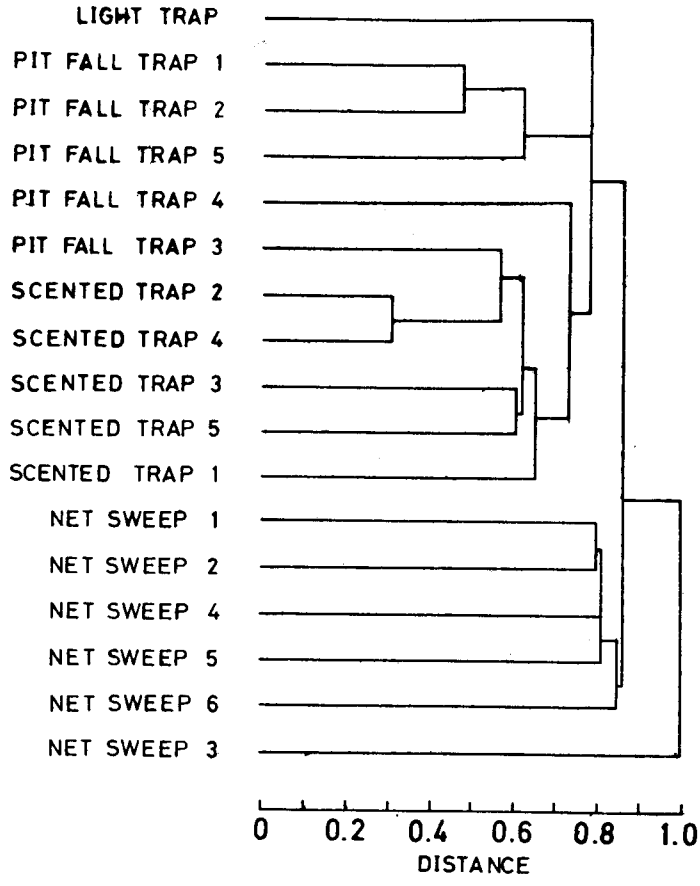

Fig.5. Dendrogram comparing insects caught by traps within a plot.
In general insects caught by the same method had greater similarity among themselves than insects caught by different methods. But insects caught in pitfall trap no. 3 were similar to those caught in the scented traps rather than those caught in other pitfall traps. Insects caught in nets weeps 3 were very different from all other insects caught in this plot. Data from plot 1.

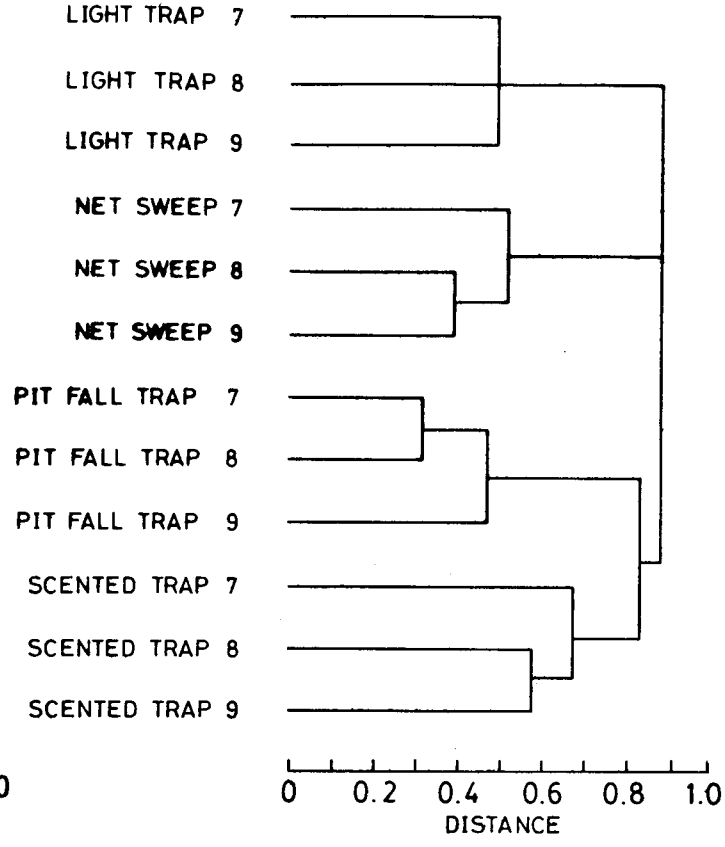

Fig. 6. Dendrogram comparing insects caught by different methods in different replicate plots of the same site.
Insects fall into four neat clusters depending on the method of trapping. Data from plots 7, 8 and 9 in Mirjan M.F.

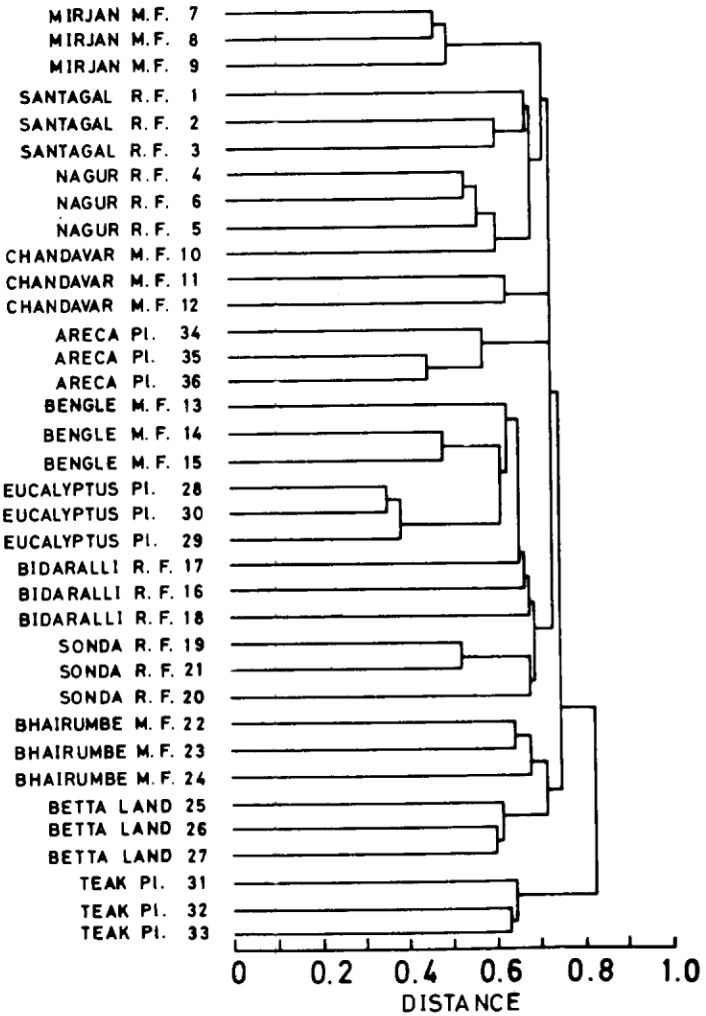

Fig. 7. Dendrogram showing similarity of insects caught in each of the 36 plots.
With the exception of Chandavar, Bengle and Bidaralli similarity between replicate plots of a site is greater than that between plots of different sites.

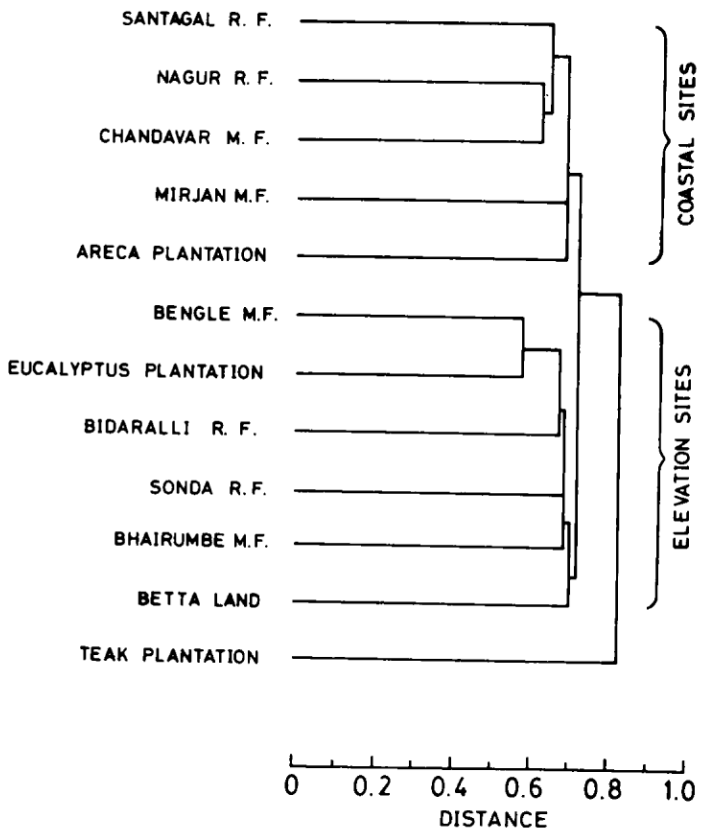

Fig. 8. Dendrogram showing similarity between different sites.
With the exception of the teak plantation all the down-ghat sites form one cluster and the up-ghat sites a different cluster.
Data pooled from three replicate plots for each site.

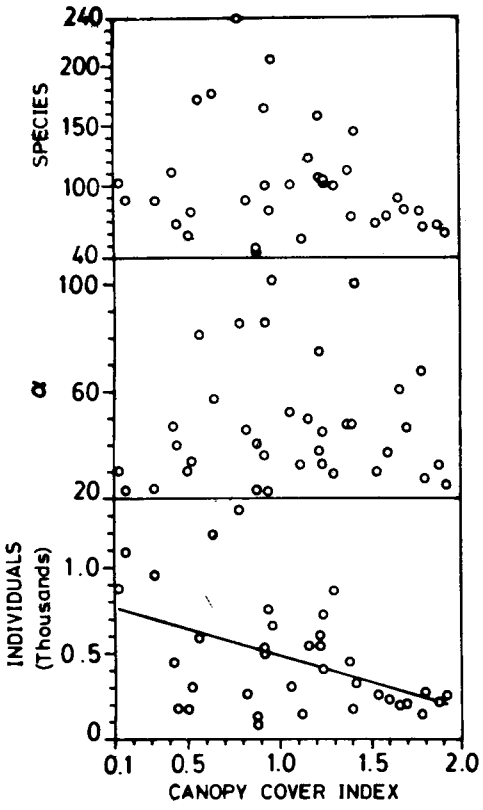

Fig. 9. Relationship between canopy cover index and number of species, α diversity index and number of individuals.
There is a significant negative correlation between canopy cover index and number of individuals (Bottom panel). (Kendalls Rank Correlation Coefficient $\tau = -0.2711$; $P < 0.05$; the straight line is given by $Y = -311.68\ x + 800.74$; $P < 0.01$). Each point represents one of the 36 plots.

are occasional exceptions. This is illustrated in an example of comparison of the 17 traps employed in plot number 1 (Fig. 5). The catches from pitfall traps 1 and 3 have a greater similarity to catches from scented traps than to catches from the remaining pitfall traps. Similarly the catch from netsweep 3 stands out as being different from everything else. These anomalies may be on account of random fluctuations in the small samples of insects caught in each individual trap.

Pooling the insects from each replicate of the same method (except of course in the case of the light traps where only one was employed in each plot) leads to fewer anomalies. This is illustrated by comparing data from each method across the three replicate plots within a study site. For most sites the pattern is as distinct as in the example shown in Fig. 6 for plots 7,8 and 9 in Mirjan M.F. It is thus clear that relatively similar insects are caught by repeating the same method in different replicate plots while relatively different insects are caught by different methods. This is by and large the pattern we find in all sites although there are some minor exceptions in some plots.

Comparison of plots and sites: Pooling catch data from all 17 traps in each plot, the 36 plots may be compared using the Morisita-Horn Similarity Index. Generally, the 3 replicate plots in each site are similar to each other and form a cluster before they "join" other clusters. This pattern was seen in 9 out of 12 sites, namely, Santagal R.F., Nagur R.F., Mirjan M.F., *Areca* Plantation, *Eucalyptus* Plantation, Sonda R.F., Bhairumbe M.F., Betta land and Teak Plantation. But there are some exceptions such as Chandavar M.F. and Bidaralli R.F. where at least one plot had greater similarity to plots from some other site than to other plots from the same site (Fig. 7).

Insect catches pooled from all methods and from the three replicate plots constitute a combined sample for a site. Such combined samples permit comparison between the habitats represented by different sites. Because the variances of α can easily be computed, it is possible to conclude that the insects caught in Bidaralli R.F. are significantly more diverse than those caught in Santagal R.F. and all other sites of lower diversity (Table 4, $P<0.05$). Similarly, insects caught in Santagal R.F. are significantly more diverse than those caught in Bhairumbe M.F. and all other sites of lower diversity (Table 4, $P<0.05$). The 12 sites are ordered according to diversity and all pairs of sites that are significantly different from each other in diversity are shown in Table 4. Pooled catch data for each site can also be used to compare the sites using the Morisita-Horn Index. This leads to the remarkable result that with the exception of teak plantation, all coastal sites form one cluster and all elevation sites form a separate cluster, although it is not clear whether this result is statistically significant (Fig. 8).

Effect of canopy cover: Reserve forests, minor forests and plantations were initially chosen because they were expected to represent different levels of disturbance. To obtain a more objective and continuous index of disturbance, however, we have

measured the extent of canopy cover in each plot. This was achieved through the canopy cover index, which is the mean number of trees whose canopies overlap with each other at any given point in the plot (see methods). Clearly, canopy cover is only one of the many factors that must affect the distribution and abundance of insects on the floor of the forests. This is reflected by the considerable scatter in points when we plot the number of species, and diversity or number of individuals as a function of the canopy cover index (Fig. 9). Nevertheless there is a statistically significant inverse correlation between the canopy cover index and the number of individuals ($P< 0.02$).There is also a suggestion that both the number of species and diversity are more variable and can reach very high levels at intermediate levels of canopy cover while relatively fewer species and lower diversity are obtained at very high or very low value of canopy cover index.

Sampling strategy: Our sampling strategy, aimed at making the methods quantitative and unbiased, involved three steps. First, we employed 5-6 replicates of each method within each plot (except in the case of light trap). Second, we employed four methods (light trap, net sweeps, pitfall traps and scented traps) within each plot. Finally, we sampled from three replicate one hectare plots within each site or habitat type (Twelve sites drawn from two elevations were sampled but this was meant to apply the underlying methodology).

In an attempt to evaluate each of these steps in our strategy, we have performed a nested ANOVA and partitioned the variance in the number of individuals of each species into the following compartments: (1) between replicates of the same method within a plot, (2) between methods within a plot, (3) between replicate plots of the same habitat type, (4) between different habitat types and (5) between elevations. Repeating this analysis separately for each of the 1,789 species, we present the minimum, maximum, mean and standard deviation of the percentage variance at each level in Table 5. On an average, 73.6% of the variance is seen between replicates of the same method within a plot, 23.7% between different methods within a plot, 1.7% between replicate plots of the same site or habitat type and a negligible amount of variance is seen between habitat types and between elevations. We conclude from this that the two most important steps in our sampling strategy required to ensure the collection of a wide variety of insects from each locality are to use replicate traps of each method within a plot and to use different methods to trap insects within each plot. Sampling from replicate plots of each site, on the average, adds only a minor component of the variance but we nevertheless recommend at least some replication of plots because in specific cases such replicate plots may be useful. For instance, in Chandavar M.F., Bengle M.F. and Bidaralli R.F. one of the three replicates was quite different from the other two (Fig. 7.)

Habitat *"Specializations:"* Comparing the relative contributions of different insect orders both in terms of number of species and in terms of number of individuals, we find that in some sites a very large proportion of the spelcies or individuals belong to one insect order and the dominant order varies from site to site. While some sites are so "specialized" others appear to be more "generalized" with a fairly even distribution of species and individuals across 4 or more orders.

A few of the relatively clear examples of this phenomenon are shown in Fig.10. 75% of all insects caught in Mirjan M.F. belonged to Coleoptera. 58% of all insects caught in Chandavar M.F. belonged to Diptera whereas in Bhairumbe M.F. 28% of the insects belonged to Hemiptera, 25% to Coleoptera, 22% to Hymenoptera and 17% to Diptera. Similarly 40% of all species caught from Mirjan M.F. belonged to Coleoptera, 38% of all species caught in the *Eucalyptus* plantations belonged to Hymenoptera but in Bengle M.F., 25% of the species belonged to Hymenoptera, 25% to Diptera, 22% to Hemiptera and 19% to Coleoptera.

Trophic structure of insect communities: Since all specimens are identified up to the family level, it is possible to determine the approximate trophic structure of the insect communities encountered in this study. Most insect families can be assigned to any one trophic level such as phytophages, predators, parasites and scavengers. The greatest difficulty in doing this was encountered in the family Formicidae. The ants have therefore been set aside as a separate category. The relative contributions of different trophic levels vary enormously. As in the case of the distribution of orders, we find that in some sites a very large proportion of the species or individuals belong to a particular trophic level and that

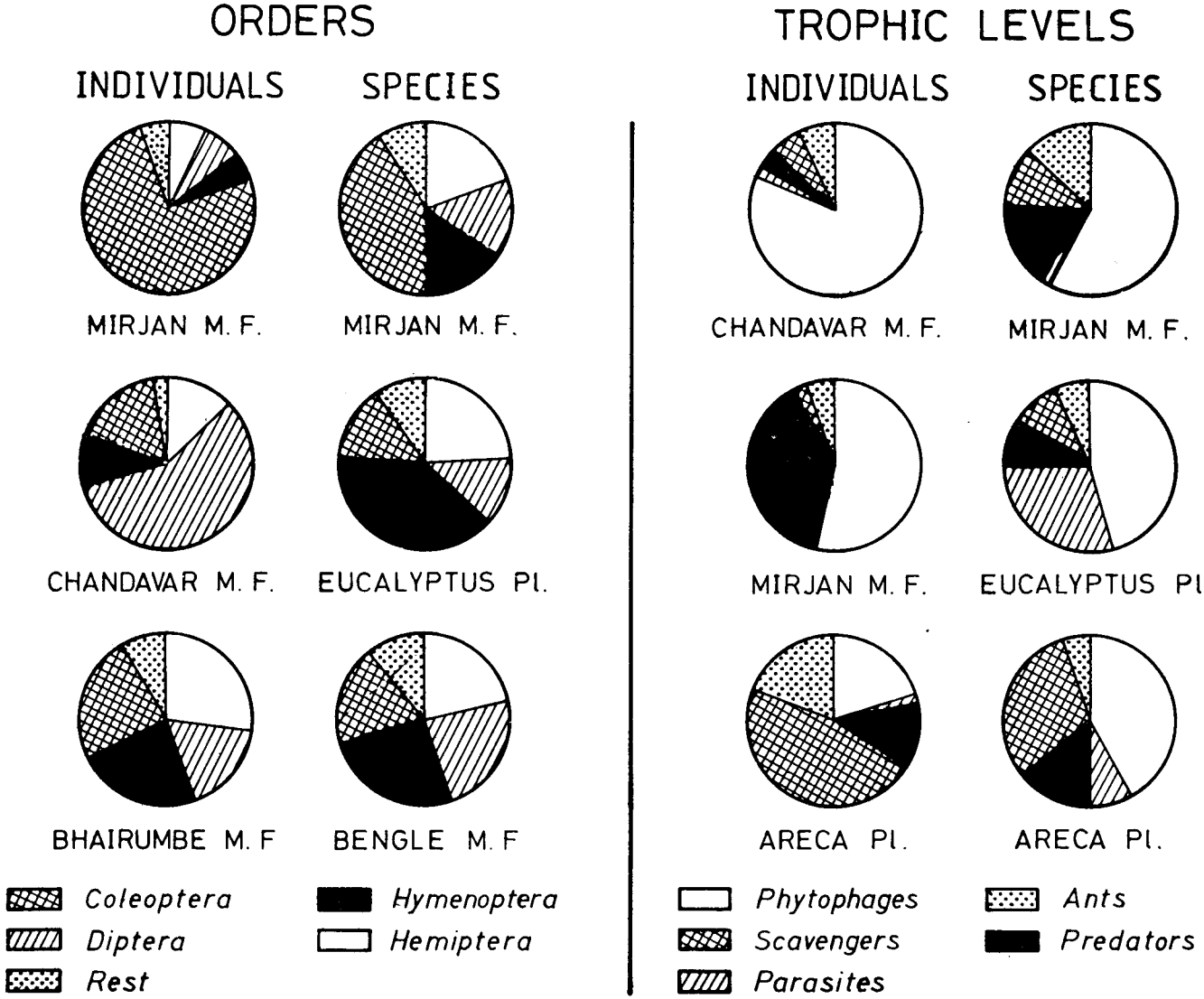

Fig. 10. Pie-charts showing the proportion of individuals and proportion of species belonging to different orders and different trophic levels in some selected sites.

TABLE 5
NESTED ANALYSIS OF VARIANCE TO PARTITION VARIANCE BETWEEN DIFFERENT COMPONENTS OF THE SAMPLING STRATEGY.

	Distribution of variance (%)			
	Minimum	Maximum	Mean	Standard deviation
Between replicates of the same method in a plot	0	99.7	73.6	37.7
Between different methods within a plot	0	100	23.7	38.4
Between replicate plots of the same habitat type	0	18.6	1.7	1.7
Between different habitat types	0	33.8	0.9	2.6
Between elevations	0	10.1	0.1	0.4

the dominant trophic level varies from site to site. A few clear examples of this are shown in Fig. 10. Nearly 82% of all insects caught in Chandavar M.F. were phytophages, nearly 54% of insects caught in Mirjan M.F. were phytophages whereas in *Areca* plantation only 20% were phytophages. Instead, scavengers account for 47% of the individuals caught in the *Areca* plantation. Ants constituted only 7% and 5% respectively of the individuals caught in Chandavar M.F. and Mirjan M.F. but constituted as much as 19% of the insects caught in *Areca* plantation.

Similar patterns can be illustrated with reference to the number of species rather than the number of individuals. Less than 2% of the species caught in Mirjan M.F. were parasites whereas nearly 29% of the species caught in the *Eucalyptus* plantation were parasites. Just as in the case of individuals, scavengers constituted a very large proportion of the species (31%) in the *Areca* plantation.

DISCUSSION

We have outlined here a strategy for quantitative sampling of insects in forested habitats and plantations that is likely to be useful to tropical ecologists with modest research budgets and minimal facilities. We argue that methods requiring the operation of a light trap continuously for months or years and especially in forested sites are inaccessible to most ecologists living and working in the tropical countries of the world. On the other hand it is studies of tropical communities that are most urgently needed and most likely to provide adequate field data required for understanding the principles of community ecology. We have therefore standardized a package of methods involving a small, portable, dry battery operated light trap and supplemented with other methods such as net sweeps, pitfall traps and scented traps. In an effort to make the methods reproducible, we have, by careful standardization, attempted to hold the sampling intensity or effort constant. One sampling unit thus corresponds to one light trap operated for a fixed number of hours in the middle of a one hectare plot, 6 net sweeps performed by a standardized method in 6 randomly chosen 10 m x 10 m quadrats, 5 pitfall traps and 5 scented traps placed at randomly chosen positions for 18 hours in a one hectare plot. Such a sampling exercise can be completed in 24 hours and therefore may be repeated every day by the same people and the same equipment. We have shown that such a sampling method yields a collection of insects which may be said to broadly represent that site. The method could thus be used to compare insect communities in different habitats or across different seasons and can also be used for long term monitoring of changes in tropical habitats (See Hammond 1990 and Stork and Brendell 1990 for similar efforts).

Traditional methods based exclusively on operating powerful light traps every night represent a very intense level of sampling compared to our methods. The result is that it is impossible to use all

the insects caught in these light traps. Most investigators are forced to discard the bulk of the catches and concentrate their attention on one or a small group of insect species. The methods we describe sample insects at a much lower intensity making it necessary and possible to use all the insects collected. Clearly, this is a more efficient procedure and leads to minimal destruction of natural populations of insects. Undoubtedly, the traditional powerful light trap method is more convenient – little or no work is required on the part of the investigators and sorting and identifying insects belonging only to a small, selected, familiar group is relatively easy. Our method requires more work on the part of the investigators both in terms of preparation and laying out the traps and more significantly in sorting all the insects belonging to different and often unfamiliar groups. Tropical ecologists will inevitably have to pay some price for not always being able to set up well organized research stations and obtain large budgets. We believe that the price in terms of man-power required by the methods we describe is small and a requirement of man-power is one price that tropical countries can pay relatively easily. Besides, the methods we have used will also help detect community level changes in the insect fauna. This is not usually achieved when only a selected group of species is monitored.

Because of the low intensity of sampling and the consequent need to include all insects collected in any analysis, we thought it best to use a variety of different trapping methods so as to attract different kinds of insects. Our finding that the catches for each of the 4 methods are quite different from each other justifies this. Because of the low intensity of sampling and the consequent small numbers of insects caught in each trap leading to random fluctuations, we thought it necessary to include several traps of the same kind in each plot and to use at least 3 replicate plots in each habitat site. Although the insects caught by the same method have greater similarity to each other rather than to insects caught by other methods in the plot, there are a few exceptions. Similarly, although the insects caught in different replicate plots of a site have a greater similarity to each other rather than to insects caught in some other site, again there are a few exceptions These exceptions justify the inclusion of replicate traps and replicate plots, but the relative rarity of these exceptions suggest that the extent of replication is fairly adequate.

In the process of standardizing these methods, we applied them to 12 carefully selected sites representing diverse habitat types so that, if the methods were successful, we might have something to say about the habitat types. We believe that the methods are successful and we therefore rank the chosen sites in their order of diversity values. The range of diversity values obtained is sufficient to permit us to make these comparisons with statistical significance.

Another interesting result we have is that with the exception of the teak plantation, the coastal and the elevation sites form 2 different clusters, suggesting that geographical separation and altitudinal variation override even extreme differences in levels of disturbance. We obtained this result in spite of including relatively undisturbed reserve forests, relatively disturbed minor forests as well as monoculture plantations both among the coastal as well as elevation sites. This is not to say that there was no difference among the various sites in one region. Several statistically significant differences in levels of diversity between sites in the same geographical region and altitude were obtained. And yet similarity between sites within one geographical and altitudinal region was greater than similarity across geographical or altitudinal regions. In addition to providing a method of understanding and comparing tropical habitats we believe that such a method, if applied on a large scale, will permit tropical ecologists to generate substantial field data relevant to current ecological theory.

For example, we have made an attempt to understand the factors affecting the distribution of diversity and abundance of insects. Using the canopy cover index as an objective and continuous measure of levels of disturbance, we have shown that the number of individuals is inversely correlated with the canopy cover index. As the canopy is opened up, we find many more insects in the forest understorey. This result is further evidence that the insects we trap are at least loosely associated and therefore characteristic of a given region. Canopy cover is clearly only one of the many factors that must affect distribution of insects. Despite the resultant scatter in the data, we have an indication that insect diversity can reach high levels at intermediate levels of canopy cover. When the canopy is closed

there is little understorey vegetation and hence, little insect activity. When the canopy is completely opened up, it results in nearly dry and barren land. It is at intermediate levels of canopy cover that a rich mosaic of habitat types can form in the forest understorey and lead to high levels of insect diversity.

The sites we have studied are different from each other in many ways. One of the more interesting differences lies in the proportional representation of species or individuals belonging to different insect orders. While some sites are "generalized" in that they have a fairly uniform distribution across 4 or more orders, others are more "specialized". For instance, Mirjan M.F. is a Coleoptera "specialist", Chandavar M.F. is a Diptera "specialist". Similarly, some sites are dominated by phytophages while others are either dominated by other trophic levels or have a relatively even representation of different trophic levels. Some sites have few ants or parasites while others have a large number of these. Why is there such a pattern in the distribution of insects ? Data of this kind will help formulate specific studies intended to understand the factors governing insect distribution. We believe that these methods will be equally useful for monitoring seasonal and long term changes in tropical habitats. Work is in progress to apply these methods in that direction.

It is now widely recognised that tropical habitats face a much greater threat of destruction than other regions of the globe. This makes the study of tropical insect communities both urgent and challenging. It is also true that the economic conditions of most tropical countries make a certain amount of developmental activity inevitable. For this reason, ecologists are being increasingly called upon to make assessments of the impact of such developmental projects on tropical biotic communities. We hope that the methods described here will contribute towards meeting these challenges.

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REFERENCES

ANSCOMBE, F.J. (1950): Sampling theory of the negative binomial and logarithmic series distributions. *Biometrika 37:* 358-382.

COLINVAUX, P. (1986): Ecology. John Wiley & Sons, New York, 725 pp.

ERWIN, T.L. (1983): Tropical forest canopies: the last biotic frontier. *Bulletin of the Entomological Society of America 30:* 14-19.

ERWIN, T.L. & SCOTT, J.C. (1980): Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: the fauna of the tree *Luehea seemannii* Triana and Planch in the Canal Zone of Panama. *The Coleopterist's Bulletin 34:* 305-322.

FISHER, R.A., CORBETT, A.S., WILLIAMS, C.B. (1943): The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol. 12:*42-58.

GADAGKAR, R. (1989): An undesirable property of Hill's diversity index N_2. Oecologia (Berlin) *80:*140-141.

HAMMOND, P.M. (1990): Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. *In:* W.J. Knight and J.D. Holloway (eds.),. Insects and the Rain Forests of South East Asia (Wallacea). Royal Entomological Society of London, pp. i-iv, 1-343.

HILL, M.O. (1973) Diversity and evenness: A unifying notation and its consequences. *Ecology 54:* 427-432.

HOLLOWAY, J.D. (1983): Insect surveys – An approach to environmental monitoring. *Atti XII Congr. Naz. Ital. Entomol.*, Roma, 1980, 239-261.

HOLLOWAY, J.D. (1987): Macrolepidoptera diversity in the Indoaustralian tropics: Geographic, biotopic and taxonomic variations. *Biol. J. Linnean Soc. 30:* 325-341.

HURLBERT, S.H. (1971): The non-concept of species diversity: a critique and alternative parameters. *Ecology 52* · 577-586.

KREBS, C.J. (1985): Ecology – The Experimental Analysis of Distribution and Abundance. Harper & Row, New York.

MARGALEF, F.R. (1958): Information theory in ecology. *Gen. Syst. 3:*36-71.

ROBINSON, M.H. (1978): Is tropical biology real ? *Trop. Biol. 19:*30-50.

SIMPSON E.H. (1949): Measurement of Diversity. Nature *163:*688.

STORK, N.E. (1988): Insect diversity: facts, fiction and speculation. *Biological Journal of the Linnean Society 35:* 321-337.

STORK, N.E. & BRENDELL, M.J.D. (1990): Variation in the insect fauna of Sulawesi trees with season, altitude and forest type. *In:* W.J. Knight and J.D. Holloway (eds.), Insects and the Rain Forests of South East Asia (Wallacea), Royal Entomological Society of London, pp. i-iv, 1-343.

TAYLOR, L.R. (1978): Bates, Williams, Hutchinson – a variety of diversities. *In:* Mound, L.A., Waloff, N. (eds) Diversity of insect faunas. Symp. Roy. Entomol. Soc. London IX, Blackwell, Oxford, London, Edinburgh, Melbourne, pp. 1-18.

TAYLOR, L.R., KEMPTON, R.A. & WOIWOD, I.P. (1976): Diversity statistics and the log series model. *J. Anim. Ecol. 45:* 255-272.

WOLDA, H. (1981a): Long-term ecological studies with light traps their practical and scientific value. *Uttar Pradesh J. Zool. 1:*1-5.

WOLDA, H. (1981b): Similarity indices, sample size and diversity. *Oecologia* (Berlin) *50:* 296-302.

WOLDA, H. (1983a): Diversity, diversity indices and tropical cockroaches. *Oecologia* (Berlin) *58:*290-298.

WOLDA, H (1983b) Spatial and temporal variation in abundance in tropical animals. *In:* Sutton, S.L., Whitmore, T.C., Chadwick, A.C. (eds) Tropical rain forest: Ecology and management. Blackwell Scientific Publications, Oxford, pp. 93-105.

WOLDA, H., & ROUBIK, D.W. (1986): Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology 67:*426-433.