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DIVERSITY AND RECOLONIZATION OF ARBOREAL FORMICIDAE AND COLEOPTERA IN A LOWLAND RAIN FOREST IN SABAH, MALAYSIA

ANDREAS FLOREN[1] AND K. EDUARD LINSENMAIR

Theodor-Boveri-Institut, Zoology III, Biozentrum, Am Hubland, D-97074 Wuerzburg

ABSTRACT. An improved method of canopy fogging was used to sample tree-specific arthropod communities of ten, five and four individuals of three understory tree species of a lowland rain forest in Kinabalu Park, Sabah, Malaysia. The authors evaluate the diversity of Formicidae and Coleoptera to identify indicators of the processes structuring the arthropod communities. In addition, ten of the trees were refogged after six months to analyze the reorganization of communities. The results showed that neither Formicidae nor Coleoptera communities showed predictable patterns in species composition or recolonization dynamics. Although the lack of predictable patterns would seem to be a consequence of a complex dynamic for Formicidae, the species pool for the Coleoptera is so large that thus far no tree-specific patterns have been identified. Communities of both taxa therefore are considered to represent non-equilibrium communities.

INTRODUCTION

Although research in tropical ecosystems has been intensified during the last ten years, we still can only speculate on the true dimensions of biodiversity in these areas. Estimates for arthropods range from 1.6 million to more than 80 million species worldwide (Erwin 1982, Stork 1988, May 1986). One of the central questions in tropical ecology today is how so many different species are able to coexist. Two types of models have been proposed to explain this question.

Deterministic equilibrium models suggest that each species can be characterized by its niche, in which it is superior to all potential competitors. Competition is seen as the key structuring mechanism leading the community to a climax state of predictable species composition (e.g., Giller 1984, Denno *et al.* 1995, Begon *et al.* 1996). In contrast, non-equilibrium models brought into discussion rather recently, suggest that competition is only of local importance, without a decisive influence on community composition (Wiens 1984). In these models, no permanent equilibrium in species composition is assumed (Chesson & Case 1986, Huston 1994). Community structure is mainly influenced by chance events (e.g., species arriving on an available resource at the most favorable time). The establishment of a species might depend on the complex interrelations of all members of the community (Pimm 1991).

Doubts regarding the general validity of the classical niche theory arose when more and more communities of the temperate regions were described as being not saturated in terms of species richness and not defineable through an equilibrium composition (e.g., Boecklen & Price 1991, Cornell 1993). Additionally, one can hardly imagine how purely deterministic mechanisms could explain the coexistence of the far greater number of species in tropical ecosystems.

To test if tropical arboreal arthropod communities show predictable (i.e., equilibrium) or non-predictable (i.e., non-equilibrium) patterns in their species composition, we investigated arboreal arthropod communities in a southeast Asian lowland rain forest. Our evaluation concentrated on the Formicidae as the most important predator group and on the guild of the phytophageous Coleoptera, among which mono- or oligophagous specialists using the respective tree species regularly, should be most easily detectable.

Our study addressed the following questions:

1. What determines the size (in terms of numbers of individuals) of arthropod communities on single trees?
2. Can the communities of ants and beetles be fully described through an equilibrium composition or do they exhibit non-equilibrium properties?
3. Does analysis of the recolonization dynamics give indications as to the processes structuring these communities?

MATERIALS AND METHODS

Field work was conducted in an undisturbed primary lowland rain forest of Kinabalu Park (substation Poring Hot Spring) in Sabah, Malaysia (6°5′N, 116°33′E). Investigation of the questions outlined above required sampling of arthropod communities of individual trees selectively and quantitatively. This was made possi-

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[1] Corresponding author.

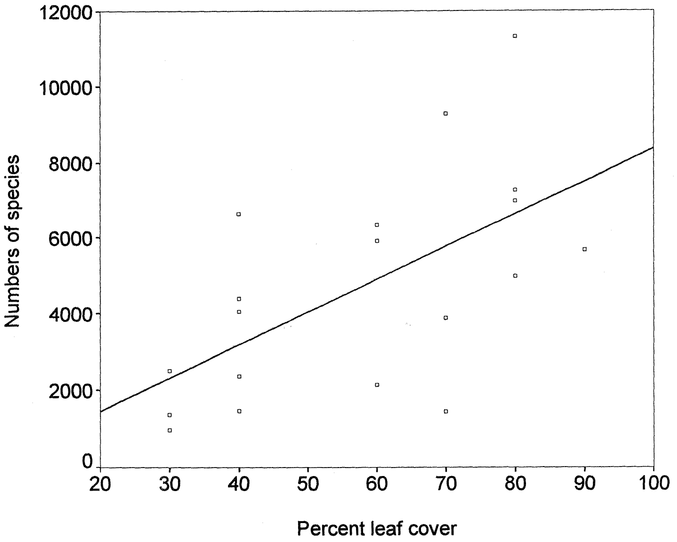

FIGURE 1. Correlation between the relative degree of leaf cover and the number of arthropods of all 19 primary fogged trees.

ble by an improved method of canopy fogging. To prevent intoxicated arthropods of the higher canopy stratum from falling into the sampling funnels, we sheltered the crown of the study tree with a 100 m^2 cotton roof. Fogging was conducted early in the morning for 10 minutes with natural pyrethrum in a concentration of 2% (for more details, see Floren & Linsenmair 1997).

Since the roof was fixed on emergent trees of about 40 meters height, we choose only trees of the lower canopy for our experiments. These were ten *Aporusa lagenocarpa,* five *A. subcaudata* (both Euphorbiaceae), and four *Xantophyllum affine* (Polygalaceae). Only trees showing a high degree of similarity one to another were selected for the experiments to keep as many factors that might influence the composition of the arthropod communities as constant as possible. For example, trees which stood in gaps, were covered by lianas, or reached well into the higher canopy and could not be sampled selectively, were not fogged.

Fogging was conducted after the rainy seasons (which last from December to February and from June to July) during four periods of field work in three years. Only one tree (*Aporusa* #8) was flowering during the fogging experiment, without a noticeable effect on the species abundance patterns within the investigated arthropod taxa. Ten of these trees were refogged after six months to investigate the recolonization dynamics. For all trees, the degree of leaf cover (estimated as projection of the leaf-covered area) and crown overlap were assessed, and tree height and girth at breast height were determined.

Community structure was analyzed by computing the alpha-diversity indices of the Hill Series, which allow analysis of the influence of dominant species on community structure (Hill 1973, Wolda 1983). In these formulas, the degree of dominance is based on the abundance of each species. The influence of dominant species on index values increases from May's to Berger-Parker's index. Using rarefaction statistics, we computed species accumulation curves, which resulted in direct comparability of the communities. For formulas, we referred to Floren and Linsenmair (1997).

RESULTS

STRUCTURE OF THE ARTHROPOD COMMUNITIES ON THE TREES FOGGED FOR THE FIRST TIME. Our results showed that the absolute numbers of arthropods within trees varied considerably. The major factor influencing the number of individuals in these arthropod communities was the leaf cover (FIGURE 1). This factor explained almost 39% of the variability in the numbers of arthropods (Spearman's rank correlation $r = 0.623$, $P < 0.004$; $R^2 = 0.3881$). No further significant correlations could be detected which might have influenced the size of a community (e.g., the height, crown volume, degree of crown overlap with neighboring trees, and presence of epiphytes).

Formicidae were found to be the dominant group in all trees. On average they contributed 54% (SD 13.62) of all individuals captured on each tree. From all trees, 192 ant species were

Table 1. Alpha-diversities arranged in the 'Hill-Series' for all firstly and refogged trees. Transformations refer to the following indices: 1/J = May; S = species number; exp. H = Shannon Wiener; 1/D = Simpson; 1/d = Berger-Parker. In addition, rarefaction values are given for size of subsample m = 200. Communities in which dominant species had changed after six months are indicated in bold.

Tree	(1/J)	(S)	(exp. H)	(1/D)	(1/d)	RAF m = 200	Dominant species
				Primary fogs			
A.l. 5	1063	25	4.43	3.27	2.58	12.59	Crematogaster #155
52	523	35	3.20	1.91	1.41	11.54	Technomyrmex #29
57	1754	21	2.00	1.33	1.16	10.56	Dolichoderus #100
62	609	26	7.64	5.36	2.87	14.19	Camponotus #115
73	3030	38	3.68	2.86	2.27	9.85	Dolichoderus #23
A.s. 8	129	52	7.06	4.73	3.22	17.39	Dolichoderus #23
50	316	34	3.81	2.30	1.60	13.16	Dolichoderus #100
51	2857	56	8.67	5.11	2.87	21.08	Dolichoderus #22
X.a. 4	1149	36	2.56	1.45	1.21	14.59	Crematogaster #44
11	2439	34	3.91	2.43	1.68	12.67	Technomyrmex #29
				Refogs half a year later			
A.l. 5	3170	39	5.32	3.72	2.35	25.96	Crematogaster #155
52	1747	31	6.96	4.94	3.16	10.56	**Dolichoderus #22**
57	1221	19	3.55	2.16	1.55	16.06	Dolichoderus #100
62	825	42	9.06	4.84	2.60	6.34	**Dolichoderus #23**
73	4964	34	2.15	1.69	1.37	19.18	Dolichoderus #23
A.s. 8	898	26	3.08	1.96	1.45	15.91	**Crematogaster #155**
50	1207	32	3.52	1.86	1.38	26.00	Dolichoderus #100
51	493	25	7.86	5.11	3.35	18.59	Dolichoderus #22
X.a. 4	2205	18	2.24	1.91	1.56	5.64	**Technomyrmex #29**
11	1250	17	2.37	2.09	1.84	5.89	Technomyrmex #29

collected during primary fogging; 80% of these species were represented by less than 20 individuals and 41% were singletons. As demonstrated by the alpha diversities of the Hill-Series (Table 1), the ant communities differed highly in dominance hierarchies from tree crown to tree crown. Even those communities dominated by the same ant species differed strongly in their overall community structure.

In addition, the highly variable rarefaction curves show that the ant communities vary in relative abundances of species in each community (Figure 2). If the community structure in all trees were similar, the curves should overlap much more. The variability of the curves is therefore a further indication of the lack of tree-specific ant communities, as well as a strong indication of the absence of a uniform deterministic structuring mechanism.

In contrast to the Formicidae, the Coleoptera showed a different pattern of species distribution. Of an estimated 2,000 species in the total sample, 1,183 thus far have been identified as morphotypes. All other species were sent to specialists for further identification. Of all beetle morphospecies, 96% were represented by less than 10 individuals and 60% by singletons. A unique and almost exclusive community of beetles was found on each tree with very little species overlap among trees. Indistinguishable from a random distribution, this finding does not give any indication that tree-specific communities of phytophageous Coleoptera exist. Neither in the fog samples nor during intensive observations within the relatively small trees did we find larvae of Coleoptera or egg clusters in large quantities. This remained true, even though the experiments were conducted at different times of the year.

Trees fogged six months later. If the reorganization of the ant communities had followed a deterministic pattern, comparison between the fog2 and fog1 communities should have given indications of such processes. Newly established communities, however, varied among themselves in species numbers, diversity and rarefaction values in a way similar to the original communities (Table 1, Figure 2). Moreover, this variability was found for all comparisons between the first and second fogs of individual trees. Large differences in community structure also were found in those communities where the same ant species remained dominant, demonstrating their limited influence with regard to species composition. In no case was the appearance and disappearance of single species in the communities predictable, and this unpredictabil-

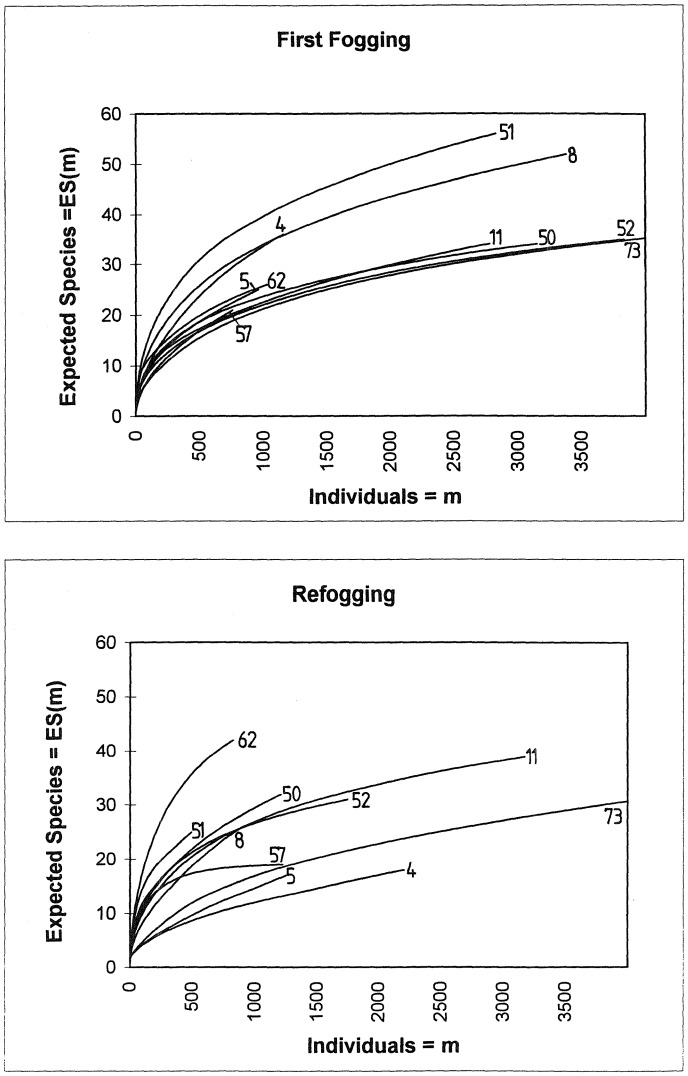

FIGURE 2. Comparison of rarefaction curves of all first-fogged and refogged trees for ant communities. ES (m) = number of expected species.

ity included species of all rank (abundance) positions.

Six months after the first fogging, the ant abundancies were distinctly lower on most trees, but no significant difference between the means of the numbers of species and the diversity values of the primary and the refogged communities could be detected. This is shown by *t*-tests for paired samples (for species numbers: $t = 1.50$, $P = 0.168$; for Shannon-diversity: $t = 0.13$, $P = 0.902$; for Berger-Parker-diversity: $t = 0.09$, $P = 0.931$).

Furthermore, we tested whether the number of species of each community had approached the original level after six months. Hypothetically, if the number of species was the same, one would find a positive correlation. No such correlation was found as is shown in FIGURE 3 (Spearman's rank correlation $r = -0.2006$, $P = 0.578$). On the contrary, we observed a regression to the mean. The most species-rich communities were composed of a smaller number of species after six months, while more species were found in originally species-poor communities.

Coleoptera showed the same distribution patterns after the refogging experiments as before. The species were always rare and showed hardly

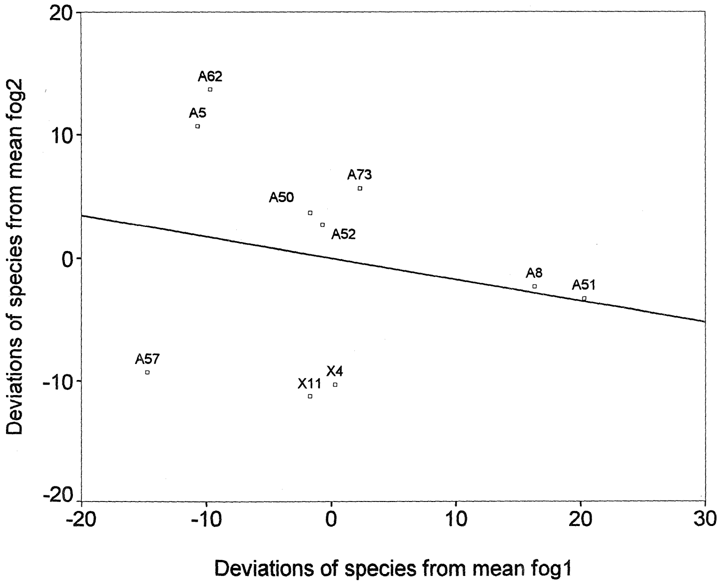

FIGURE 3. Correlation of the deviations in species numbers from their particular mean of all first and second fogs (mean species Fog1 = 35.7, SD 11.13; mean species Fog2 = 28.3, SD 8.77).

any overlap among trees. Even after pooling the beetles of all first fogs and refogs (all 8,856 specimens), we could observe no indication of species saturation. Similar to the ant patterns, the differences in the means of the Coleoptera numbers were not significant (t = 1.30, P = 0.225), and we found no correlation between the species numbers and the individual trees after six months (Spearman's rank correlation r = 0.3079, P = 0.387).

DISCUSSION

Our results show that the crowns of all trees investigated were structurally quite similar. Thus, all trunks of the *Aporusas* were hollow in the upper crown area and had accumulated detritus and dead wood (their own and other material dropped into the trees). Epiphytes, rare in all trees, were therefore neglected as a structural parameter. For reasons not yet understood, epiphytes are much less frequent in southeast Asian forests than in the neotropics. The only parameter that varied largely between trees and which correlated significantly with the number of arthropods in a tree crown was the degree of leaf cover. This result could be explained in different ways. Dense crowns might be simply more 'resistant' obstacles which could filter insects from the air in larger quantities than trees with a less dense canopy. On the other hand, insects could actively seek these crowns as they might offer more opportunities for finding food and protection.

Among the highly diverse Coleoptera, the central result was the rareness of all species. On the basis of our samples, we could not identify tree-specific associations which would be expected by deterministic models of community structure. These results are very characteristic for tropical lowland rain forests and correspond with all comparable investigations (Wagner 1996, Stork *et al.* 1997). Analysis of recolonization dynamics on trees that had been refogged several times on consecutive days suggests that most arthropods do not stay very long in the trees. For Coleoptera, for example, we found an almost total species turnover after every fogging experiment (Floren & Linsenmair 1998). Since, however, no data are available that consider the recolonization dynamics of undisturbed tree crowns, this discussion can be only a preliminary one.

Formicidae, as the most prevalent group of predators in lowland rain forests (Fittkau & Klinge 1973, Hölldobler & Wilson 1990) might have special impact on the structure of arboreal arthropod communities. The omnipresent ants could be responsible for the high dynamic community composition of arthropods by maintaining a high predation pressure. Thus, we found almost exclusively highly mobile species in all communities. We also never found large quantities of egg clusters which might indicate that herbivores use the tree crowns for feeding but not for egg laying . Given the small sample size, we cannot yet evaluate this proposition.

The only arthropod species that was found in high abundancies on all *Aporusa* trees, and thus obviously unaffected by the ants, was a tingid bug (genus *Physatocheila*). Many tingids are known to possess quite effective chemical defenses, and the species we collected most probably possess such defenses (Scholze pers. comm.). We have not found definite indications, however, that the arthropods in our study used chemical defenses.

Our results contrast with those on community composition of trees in temperate ecosystems in which ants, only under special circumstances, reach such abundancies that they influence the structure of arthropod communities (Grant & Moran 1986, Whittaker 1991). Consequently, immobile phytophageous species can always be found in high abundancies and with predictable community structure in temperate ecosystems (e.g., Southwood *et al.* 1982, Hsiao 1985, Floren, unpubl. fogging data).

Unlike other arthropods, ants and ant nests are found abundantly in the southeast Asian trees providing us data that could be analyzed in detail. As for the other groups of insects, the community structure (at the level of morphospecies) was very variable, without any indication of a uniform structuring mechanism (see also Floren & Linsenmair 1997). One should expect, however, that dominant species mutually exclude each other, at least in part, under the preponderance of deterministic structuring mechanisms. Dominants should control larger territories and exert a stronger influence on the community leading to a similar species composition (Hölldobler & Wilson 1990). Indications of this, however, were never detected (see also Götzke & Linsenmair 1996). In just 19 trees investigated, we observed seven different ant species, dominant in their communities. Although most trees had direct contact with other trees, and thus territories spanning over several canopies potentially could be established, we never observed this. Furthermore, baiting experiments and observations inside the tree crowns showed that a dominant species was unable to monopolize the crown in which it was nesting or exclude other species effectively from the baits (Floren 1996).

Other indications of the lack of classical deterministic structuring mechanisms come from the analysis of the recolonization data. According to classical conception, the original communities should have been dominated by species that were good competitors, since no recognizable large disturbances have occurred during long periods of time. In the long run, communities that have been undisturbed should develop to a similar climax composition. In the presence of dominant species, the establishment of an ant mosaic would be expected, as found in disturbed systems (i.e., Leston 1973, Jackson 1984). Climax communities develop through various stages of succession, identifiable by specific species sequences (Majer 1993). In particular, communities sharing the same dominant species should be structured in a similar way indicated by similar diversities and similar shapes of rarefaction curves. In our study, the reorganized ant communities after six months were equally variable in their species composition compared with communities in the primary fogged trees. Only the total number of individuals was found to be lower on most trees, presumably because of the slow growth of newly founded or recovering nests. Although a multitude of successful species colonizations occurred during the time of community reorganization, we could not identify either pioneer or climax species. Nor could we identify any predictable effect of the newly established dominant species on the community structure.

In particular, the first fog did not lead to a significant decrease of the species numbers and diversity. Instead, a regression toward the general mean was apparent, e.g., trees with originally low species numbers had a higher species number at refogging, while trees with originally high diversity recollected a smaller number of species. Even when based on ten samples only, this result is a further indication of the role of stochastic events in the species composition of a community. The species composition in the ant communities investigated therefore are apparently the result of a very complex dynamic (Hastings *et al.* 1993). In addition, the regression to the mean might indicate the existence of a species saturation for individual trees and might hint that species composition at the functional level is not random. The stability of a community, however, could grow with increasing age and species number (Pimm 1991); the species composition would then depend on the unique history of a community. To test this hypothesis, the insect communities on the trees investigated should be refogged in a few years.

The fractions of rare species among Coleoptera remained extremely high also on refogged (e.g., recolonized) trees. With regard to the dynamics of the beetle communities, this observation indicates that beetle communities probably are not interactive (Cornell & Lawton 1992). Classical deterministic models, however, are definitely not able to explain this pattern.

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