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CHANGES IN ARBOREAL ARTHROPOD COMMUNITIES ALONG A DISTURBANCE GRADIENT

ANDREAS FLOREN* AND K. EDUARD LINSENMAIR

Theodor-Boveri-Institut, Zoology III, Biozentrum, AM Hubland, D-97074, Wuerzburg, Germany.
E-mail: Floren@biozentrum.uni-wuerzburg.de

ABSTRACT. Arboreal arthropod communities in four forests along an anthropogenic disturbance gradient in Malaysia were sampled by fogging and changes at the ordinal level were analyzed. At least ten individuals of a single tree species from each forest type were fogged. These were two species of Euphorbiaceae from the primary forest and from the most disturbed forest, and a species of Verbenaceae in the two other secondary forests. The high constancy and low variance of the relative proportions of taxa in the crown communities found in primary rain forests was lost in the disturbed forests. Anthropogenic disturbances (e.g., extended clearings) led to fluctuations in rank abundances of taxa. The Formicidae lost their dominant rank in the most disturbed forest while Lepidoptera larvae, which were always rare in the primary forests, reached high abundances. During forest succession, the composition of taxa in the communities converged to the conditions of the primary forests. Short term colonization processes, which were investigated in every type of forest by carrying out five daily consecutive foggings of an individual tree, always displayed great variability. Coleoptera and Diptera, in addition to non-formicid Hymenoptera in the five-year-old forest, were dominant. During all daily foggings it was unforeseeable which group would be present in high numbers. This leads us to suppose that particularly strong stochastic influences are in effect during short term colonization.

Key words: tropical rain forest, arthropods, community dynamics, canopy fogging, disturbance gradient

INTRODUCTION

Tropical lowland rain forests, despite their high diversity, are being destroyed worldwide (Turner & Corlett 1996). Little information is available about how these ecosystems function. Thus, it is not understood to what extent the maintenance of this species richness is a consequence of a deterministic structuring or whether non-equilibrium processes are of significance (Chesson & Case 1986, Terborgh 1992, Pimm 1991, Huston 1994). During many years, we have studied the composition and dynamics of arboreal arthropod communities of conspecific trees of mature lowland forests (Floren & Linsenmair 1997, 1998, 1999, Horstmann et al. 1999). Besides studying primary forest we are investigating the changes in tree communities following strong anthropogenic disturbances. Previous research was mainly botanical (e.g., Leigh et al. 1993, Nepstad et al. 1996, Pinard 1996, Dupuy & Chazdon 1998) or related to higher systematic taxa (e.g., Lawrance 1994, Mason 1996). Few studies, however, looked into the consequences of disturbance to arthropod communities (but see Roth et al. 1994, Daily & Ehrlich 1995, Eggelton et al. 1996, Olson & Andriamidana 1996, Holloway 1998, Lawton et al. 1998).

Here we report changes in arboreal arthropod communities at the ordinal and in part the familial level, of four forests with different levels of disturbance. Furthermore, we present data on the short term colonization dynamics of some arthropod taxa in each forest type. Analysis at the morphospecies level is currently being worked out and will be published elsewhere.

MATERIALS AND METHODS

Field work was carried out in Kinabalu National Park in Sabah, Malaysia, which extends around Mt. Kinabalu with an area of 754 km^2. We chose four forest types, a lowland dipterocarp hill forest, which was relatively undisturbed by humans, and three ages of regenerating forests. The regenerating forests had been cleared for crop planting 5, 15, and approximately 40 years ago (here termed, respectively, SI, SII, and SIII). These forests were adjacent to one another and after some kilometers merged into primary forest. Our initial aim was to investigate the arthropod communities of a tree species occurring in all types of forest. Since we did not find such a tree species, we chose an unidentified but frequent pioneer tree (Euphorbiaceae) in SI, and the tree *Vitex pinnata* (Verbenaceae) from SII and SIII. From SI and SIII ten trees were fogged, eleven trees from *Vitex pinnata* was common in the SII forest but markedly rarer in the SIII forest. From the primary forest, 10 *Aporusa lagenocarpa* trees (Euphorbiaceae), which had been

* Corresponding author.

sampled in an earlier investigation, were chosen for comparison. In addition to the frequency of the investigated tree species and in order to allow comparison of the communities, it was noted that all trees of a forest type showed greatest similarity in structural tree parameters (e.g., the occurrence of epiphytes, lianas, crown density, and crown overlap with neighboring trees). The pioneer trees of SI, with a mean height of 6 m, were distinctly smaller than all *Vitex pinnata* trees, which measured around 20 m high. *Aporusa lagenocarpa* trees of the primary forest reached 25 m, though not extending 30 m in height.

To allow selective sampling in the multilayered primary forest, tree crowns were covered with a large cotton roof. This prevented sampling intoxicated arthropods from larger neighboring trees. A detailed description of this selective canopy fogging is given in Floren and Linsenmair (1997; see also Stork et al. 1997 or Adis et al. 1998). Because of the simpler forest structure in the secondary forests which had no closed canopy, and in which no distinct crown layer had yet formed, it was possible for us to do our sampling without the roof construction. In every case enough funnels were installed beneath the trees that 80–90% of the crown projection area was covered. The arthropods caught were stored in ethanol and sorted to the ordinal level in the laboratory. Evaluation concentrates on the more prominent orders.

The composition and changes of the relative proportions of taxa in the communities were compared with a one-way-ANOVA (this required in some cases a log-transformation of the data). A following post-hoc test (Scheffe's test) was used for the multiple pairwise comparisons between taxa. If the preconditions for computing these tests had not yet been fulfilled, a Mann-Whitney *U*-test was conducted instead. This was the case for the taxonomic comparison within SII as well as the comparisons of relative frequencies of Diptera and Lepidoptera larvae between the forests. We set the significance level for this to $\alpha < 0.001$.

RESULTS

Arthropod Communities

To illustrate the changes in the taxonomic composition of the arthropod community, we concentrated on those taxa already known to occur regularly in trees and were obtainable through fogging (Floren & Linsenmair 1997). FIGURE 1 shows the different proportions of taxa in the communities of each forest.

Variability in taxonomic abundance in all disturbed forests was so large that significant differences were only found in single cases (among the "other Hymenoptera" and Heteroptera, which were always collected in low numbers, and the remaining taxa). Exceptions were the Homoptera in SI, whose relative proportions were significantly lower than other taxa ($P < 0.001$) as well as the Formicidae in SII and SIII, which were most abundant on all trees. In contrast, abundance fluctuations were less prominent for most taxa in the primary forest, and a characteristic taxonomic composition was always evident. Here, Formicidae differed significantly from all other taxa ($P < 0.001$) and Lepidoptera larvae at least at the 0.01 level.

Differences Among Forests

Among the forest types we found large differences in the relative proportions of Formicidae, Coleoptera, Lepidoptera larvae, Homoptera and, less distinctly, in the "other Hymenoptera." The relative proportions of Diptera, Heteroptera, and Arachnida did not differ among forests (see TABLE 1).

The multiple pairwise comparisons confirm that the Formicidae were distinctly less abundant on pioneer trees in SI compared to the other forests ($P < 0.001$). Their numbers in SII were not significantly different from those of the primary forest. Coleoptera, and to a lesser extent "other Hymenoptera" showed significant differences between SI and SII ($P = 0.008$ and $P = 0.033$ respectively), as well as between SI and the primary forest ($P = 0.000$ and $P = 0.027$, respectively). In addition, the proportions of Coleoptera differed between SIII and the primary forest ($P = 0.027$). With increasing time of regeneration Homoptera reached around 5% in each community. A significant difference was detected between SII, in which Homoptera were most numerous, and the primary forest ($P = 0.002$), while no difference was found between SII and SIII ($P = 0.182$) as well as between SIII and the primary forest ($P = 0.428$). Significant differences for the Diptera were found between SII and SIII ($P = 0.005$) as well as between SIII and the primary forest ($P = 0.015$) which, because of the alpha correction, were not considered significant.

Relative proportions of Lepidopteran larvae did not differ among disturbed forests ($P < 0.001$). SI and SII were highly significantly different to the primary forest ($P < 0.001$), and SIII on the 0.01 level. However, a decrease of mean values can be seen which is recognizable in the minimum/maximum values of the relative proportions of the Lepidoptera larvae on the trees

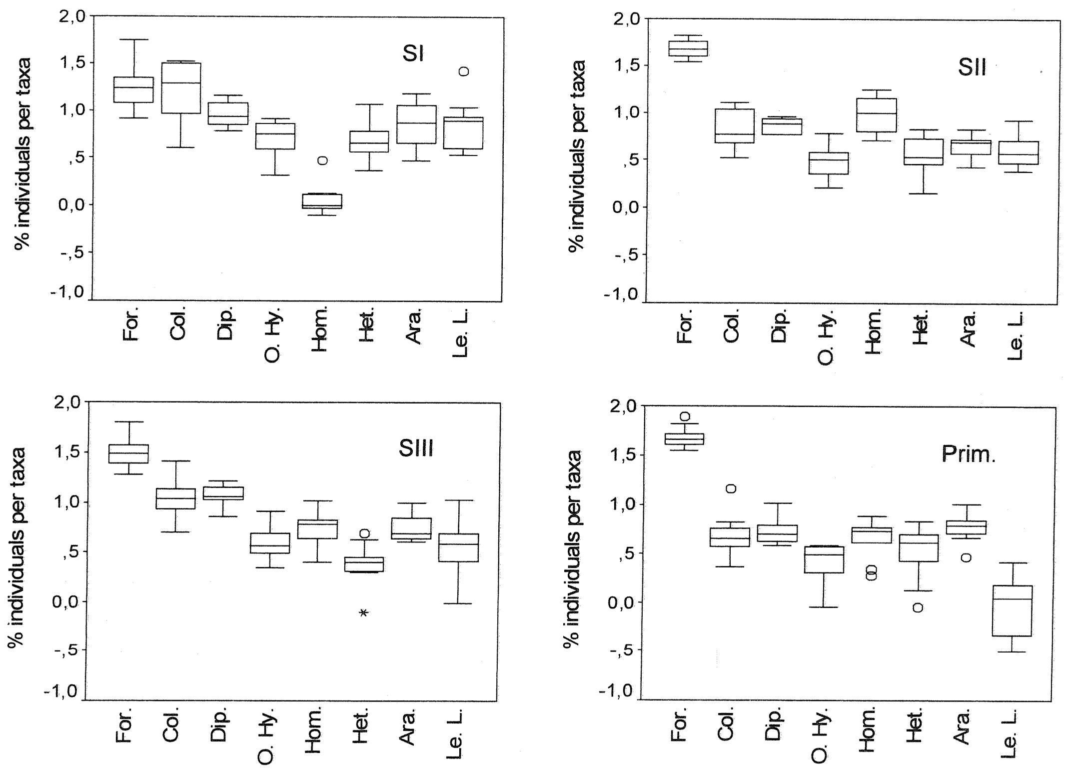

FIGURE 1. Relative composition of taxa on trees in forests of different disturbance levels. Prim.: Primary forest. SI, SII, SIII: are forests which regenerate since 5, 15, and 40 years. Y-axis on a log scale. For. = Formicidae, Col. = Coleoptera, Dip. = Diptera, O.Hy. = other Hymenoptera, Hom. = Homoptera, Het. = Heteroptera, Ara. = Arachnida, Le.L. = Lepidoptera larvae.

(Prim. 0.31–2.61%; SI 3.47–26.87%; SII 2.46–8.36%; SIII 0.98–10.76%).

Daily Foggings

The results of our studies on the short term colonization in all forest types is shown in FIGURE 2. Formicidae and Heteroptera abundances on the pioneer trees of SI decreased continuously in the course of the foggings. In contrast, numbers of Coleoptera, which were represented with 72 specimens in the first sample, increased to 909 and then dropped to 706 and 642 individuals, respectively. Even after the fifth fogging we counted 234 beetles, still distinctly more compared to the first fogging sample. As a con-

TABLE 1. Means and standard deviations of relative proportions of arthropod taxa in the forests investigated. In addition, results of forest comparisons are given; NS = not significant, ** = $P < 0.01$, *** = $P < 0.001$. For Diptera and Lepidoptera larvae a Kruskal Wallis ANOVA was computed.

	Prim.		SI		SII		SIII		ANOVA	
	MW	SD	MW	SD	MW	SD	MW	SD	F	*P*
Formicidae	45.02	15.97	21.01	14.61	48.48	9.54	33.59	12.70	8.967	***
Coleoptera	6.09	3.39	20.09	11.43	7.47	3.53	12.09	5.79	9.357	***
Diptera	8.85	6.87	9.30	2.87	7.80	1.81	12.10	3.07	10.670	NS
Other Hym.	3.31	1.24	5.52	2.17	3.21	1.37	4.41	2.09	4.462	**
Homoptera	4.50	1.85	1.25	0.63	9.69	4.64	5.91	2.12	37.461	***
Heteroptera	6.14	4.76	5.35	2.71	3.93	1.68	2.69	1.17	2.710	NS
Arachnida	5.62	1.98	8.08	4.18	4.69	1.30	5.85	2.02	2.410	NS
Lepid. Larv.	1.19	0.80	8.81	6.77	4.35	1.75	4.49	2.89	29.466	***

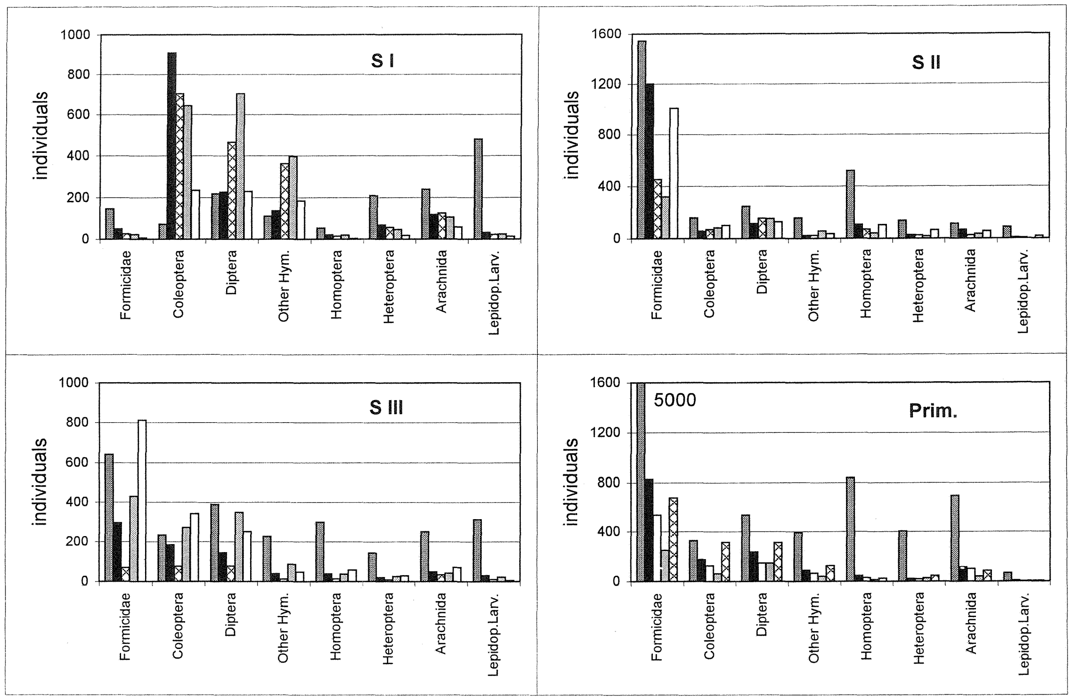

FIGURE 2. Short term colonization dynamic in all forests investigated. From every forest a single tree was fogged five times on consecutive days. Each of the five bars for each taxa represents a single fog.

sequence, the relative proportions of Coleoptera increased from 4% to 50% and remained constant during the following foggings at around 30%. The Diptera also were found during the consecutive foggings in larger numbers compared to the first sample and correspondingly their relative importance increased from 5% to 30%. Extraordinarily numerous in SI were nonformicid Hymenoptera which could account for 20% of all arthropods. As already mentioned for the primary fog, Homoptera remained rare during the consecutive foggings in SI and their relative proportions dropped continuously to 0.5%. As expected, the proportions of the low mobility Lepidoptera larvae decreased from 480 individuals (almost 27%) to 8 individuals after the last fog (1.5%). Arachnida, with a high potential of colonization, always contributed around 5% to the communities.

Abundances of many taxa in forest types studied did not decrease continuously during the foggings. However, on certain days, they could increase markedly in numbers in any of the foggings. This was without evident cause, as neither the method nor the climatic conditions changed compared with the previous days. Again, species of Coleoptera and Diptera were always the first to arrive in the tree crowns. While many more Diptera than Coleoptera were found during the consecutive foggings in SII, Coleoptera equaled or exceeded the number of Diptera in SIII.

DISCUSSION

Composition of Arthropod Communities

Arthropod communities in the primary forest were of regular composition at the high taxonomic level (FIGURE 1, TABLE 1), with consistent relative proportions of taxa (Stork 1991). All trees were dominated in numbers by Formicidae. Relative proportions of Coleoptera, Diptera, Homoptera and Arachnida were not significantly different from each other, but were different with respect to the Lepidoptera larvae (compare Floren & Linsenmair 1997). Among the Coleoptera we have shown that the same families (Chrysomelidae, Curculionidae, Staphylinidae) and genera were always most numerous in the tree crowns (Floren & Linsenmair 1998). Larger fluctuations in abundances were detected within the group of "other Hymenoptera" and Heteroptera. However, in a larger sample their mean lay around 3%, and differed significantly to the other taxa (Floren & Linsenmair 1997). This pattern of community organization changed markedly in the most disturbed forest type SI. During forest regeneration, arthropod community structure at the ordinal level approximated the conditions of the primary forest. Thus, Formicidae were again the dominant group in the trees of SII. The presumed high predation pressure they exert could be responsible for the lack of low mobility arthropods in the primary forest (Floren & Linsenamir 1997, 1998, 1999). This was confirmed by a further 39 foggings of another ten tree species (Floren unpubl. data). Lepidoptera larvae were still found even after 40 years at an average of 4% in the trees, however, they showed a clearly recognizable decrease during forest regeneration. We suspect that the ant communities in the secondary forests still consist in small numbers of predatory species which do not exert a comparably high predation pressure. In order to test this, however, autecological studies are necessary which exist for few species. Where the many herbivorous species in tropical lowland forests develop is a question which needs further investigation.

In all secondary forests most the other taxa investigated showed no distinguishable pattern because of their large fluctuations in abundances (TABLE 1). To what extent the lack of Homoptera in SI is generally characteristic for this forest type, can not be presently determined. For this, a larger sample and the observation of additional tree species is necessary. It was, however, rather surprising because large numbers of Homoptera have often been found in strongly disturbed systems (e.g., Jackson 1984, Werner pers. comm.; unpubl. data). The mass occurrence of Homoptera in young regeneration forests is also known from temperate zones, however, not from primary-like old forests (Schowalter 1988, 1995).

Even after 40 years of forest regeneration distinct differences in arboreal arthropod communities of primary forest are obvious. Besides the mentioned changes at the ordinal level, the abundance patterns of many species is evident (Floren & Linsenmair unpubl. data). A presorting of morphospecies shows that within Coleoptera and the "non-formicid Hymenoptera" (Horstmann pers. comm.) single species were highly abundant in the secondary forests. During forest succession these species became more and more rare, and in the primary forest all collected species were always rare (Floren & Linsenmair 1998, 1999, Horstmann et al. 1999). Convergence of the arthropod communities progresses relatively slowly, even when the disturbed forests were in direct contact with the adjacent primary forest. This is probably caused by the large differences in forest structure and the correlated changes of microhabitat conditions which drastically differ also after 40 years from those of the mature forest (Turner & Corlett 1996). This may act like an effective filter for many arthropods. Exactly how diversity changes with the regeneration of structural heterogeneity has yet to be studied.

Short-term Colonization Dynamic

The results of consecutive daily foggings (FIGURE 2) document a very high short term colonization dynamic in every forest type in which Coleoptera and Diptera were dominant in numbers. Among those we found the fastest new arrivals in the tree crowns. A group with a constant high colonization ability was the Arachnida, probably a consequence of their passive dispersal through the air. The large increase in numbers of non-formicid Hymenoptera during the consecutive foggings in SI was remarkable, which remained of distinctly less importance in the other forests. The Homoptera, in contrast and in spite of their potentially high mobility, did not play an important role during the short term colonization.

A phenomenon not yet understood is the large increase in numbers of individuals within single taxa during the consecutive foggings in all forest types, independent of whether species are good or bad colonizers. This may indicate that other factors, for example weather, that have not been recognized, strongly influence the colonization dynamics. The degree to which individual taxa would be involved in the colonization dynamic was typically unpredictable. This points to the importance of stochastic effects during short term colonization. Such effects were confirmed for the Coleoptera communities in primary forest (Floren & Linsenmair 1998). In contrast to the disturbed forests, however, all species remained rare in the communities in the mature forest. A comparable dynamic was found in an oak plantation forest in Germany (Floren et al. unpubl. data), indicating here too, a greater significance of random effects in forests of the temperate zones than previously assumed.

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