ECOTROPICA 7: 33–42, 2001

DIVERSITY OF ORTHOPTERA FROM BORNEAN LOWLAND RAIN FOREST TREES

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Abstract. The composition and colonization dynamics of arboreal Orthopteran communities were studied in a SE-Asian mixed dipterocarp lowland rain forest by insecticidal fogging, re-fogging after different periods of time, and by stem eclectors during different times of the year. In total, 2324 Orthoptera were collected by fogging, of which 87.3% were nymphs. Imagines were sorted to 49 morphospecies, of which 47 (96%) were new to science. Almost 50% were singletons, and only three species, all belonging to the omnivorous subfamily Mogoplistinae (genus *Ornebius*), occurred with more than 10 adult individuals. Orthoptera seemed to be randomly distributed in the canopy without showing any host-tree-specific adaptation. This is also indicated by the re-foggings, in which Orthoptera colonized the trees, according to the relative proportions of subfamilies and feeding guilds occurring in the canopy. No pioneer or climax species could be distinguished. In the stem eclectors 787 specimens were caught, of which 98.2% were nymphs, mostly first and second instar, indicating migration into the canopy after egg development in the soil or lower forest strata. In contrast to the numerous nymphs of hemimetabolous taxa, less mobile arthropods, mainly larvae of holometabolous groups, were almost completely lacking in the canopy. This is probably due to the high predation pressure of the ants which influence community composition.
Accepted 9 July 2001.

Key words: *Ant predation, canopy fogging, colonization dynamics, diversity, hemimetaboly, stem eclectors.*

INTRODUCTION

The existence of an extremely diverse arthropod fauna in the canopy of tropical lowland rain forest, as first suggested by Roberts (1973) and Erwin (1982), has since been confirmed by various investigations (references, e.g., in Stork *et al.* 1997, Linsenmair *et al.*, in press), raising the question of how such high diversity is maintained (e.g., Beaver 1979, Huston 1994, Linsenmair 1995, Pianka 1996, Price *et al.* 1995, Rosenzweig 1995). This is the focus of our project in SE Asia that aims at understanding the mechanisms structuring arboreal arthropod communities. In this paper we consider the Orthoptera, which usually account for between 1 and 3 % of the specimens in tree communities (Stork 1991, Floren & Linsenmair 1997, Wagner 1997). In contrast to previously analyzed insect orders from the canopy, Orthoptera are hemimetabolous. Their nymphs are usually highly mobile and basically belong to the same feeding guild as the adults. Two major groups of Orthoptera can be distinguished: the Caelifera ("grasshoppers") which are diurnal and herbivorous, showing all varieties of the specialist-generalist continuum (Rowell 1978), and the Ensifera (mainly "katydids" and "crickets") which are nocturnal and comprise a wider range of feeding habits, including herbivores, predators, and omnivores. To date, most studies have focused on Neotropical Caelifera, which were collected either by fogging (Roberts 1973) or tree-felling, and netting of grasshoppers at ground level (Descamps 1978, 1981). Those studies revealed a species-rich canopy fauna and gave the first insights into community structure, resource partitioning (Amédégnato 1997), and ethology (Riede 1987). Although the Ensiferan fauna of trees is generally much more diverse than the Caeliferan fauna, the arboreal Ensifera remain largely unstudied. Here we present for the first time an analysis of complete Orthopteran communities from trees in a SE-Asian lowland rain forest, which were sampled by fogging, re-fogging, and stem eclectors. We describe the Orthoptera fauna associated with three tree species, in terms of their diversity and re-colonization

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dynamics (of the primary fogged trees) and ask how important tree trunks are as pathways for canopy colonization. Furthermore we investigate whether differences in life history features of holometabolous and hemimetabolous taxa have an effect on the structure of tree-dwelling communities.

MATERIALS AND METHODS

Study site and sampling procedures. Investigations were conducted in Kinabalu National Park, substation Poring Hot Spring, Sabah, Malaysia, Borneo (6°5'N, 116°33' E), in a floristically rich mixed dipterocarp lowland forest (500 to 700 m a.s.l.). The region is characterized by a typical tropical climate with at least 2000 ml precipitation per year (Kitayama 1992, Pfeiffer 1997). All investigations were done after the rainy seasons (which last from February to May and August to end of November) during four field stays between 1992 and 1993.

An improved method of canopy fogging was used to sample arthropod communities associated with individual trees. Since methodical details have been published elsewhere we give only basic information here (Floren & Linsenmair 1997, 2000). The trees were fogged for ten minutes with natural pyrethrum used as insecticide early in the morning and all arthropods that had dropped into the funnels after two hours following fogging were used in the analysis.

Nineteen medium-sized trees of the canopy understory, representing three species from two families, were fogged. These were ten *Aporusa lagenocarpa*, five *A. subcaudata* (both Euphorbiaceae), and four *Xantophyllum affine* (Polygalaceae) (we recognized only during the investigations that the Euphorbiaceae trees belonged to two species). *A. lagenocarpa* was the only species that occurred in larger numbers in our research area of which sufficient available individuals were found that were not covered with lianas. All trees were smaller than 30 meters in height and similar with respect to insect habitat conditions, for example concerning the existence of stem cavities, dead wood, and detritus accumulations, etc.; epiphytes were almost completely lacking (Floren & Linsenmair 1998a). Only one *A. lagenocarpa* flowered during one sampling period, however, without a noticeable effect on the species abundance patterns. All trees showed continuous leaf flushes of low intensity. Ten trees (five *A. lagenocarpa*, three *A. subcaudata*, and two *X. affinae*) were re-fogged at least after six months, two *A. subcaudata* trees were fogged again after a week, and one *A. lagenocarpa* tree was re-fogged on four consecutive mornings.

Stem photo-eclectors (emergence traps) were installed on 47 tree trunks at 4 m height in order to quantify arthropod immigration into the canopy along tree stems from the ground (these were 35 *A. lagenocarpa*, 4 *A. subcaudata*, 4 *Depressa nervosa* (Guttiferaceae), and 4 unidentified trees. Their bark was only slightly structured and not covered with thalloid epiphytes. For the operational method of the eclector-traps see Basset *et al.* (1997). The traps were filled with 4% formalin solution and emptied every two weeks. A total of 171 samples was evaluated.

Arthropod sorting and data analysis. Orthoptera were separated and sorted to morphospecies by one of us (SI). However, most of the nymphs could be identified only to subfamily level, therefore evaluation is only based on adults. Classification followed the Orthoptera Species File (Otte & Naskrecki 1997). Specimens from the studies have been deposited in the Museum Koenig, Bonn or in the institutions mentioned in the resulting taxonomic publications. In addition, various persons kindly provided data from hand collecting and light-traps which were contrasted with the fogging material.

Shinozaki curves were calculated to compare communities at the beta-diversity level (Shinozaki 1963, Achtziger *et al.* 1992). These are expected species accumulation curves and their steepness provides information about the overall completeness of the sampling effort (a more comprehensive discussion is given in Floren & Linsenmair 2000). In addition, Soerensen's index was used to measure similarity in species composition between communities (Magurran 1988). For a between comparison, the fogging data were standardized for a crown projection of 1 m^2 and a leaf cover of 100%. Bonferroni's correction was used to adjust the level of significance for multiple pairwise comparisons (Lehmacher *et al.* 1991).

RESULTS

A total of 2324 individuals of Orthoptera was obtained by fogging. The number of specimens collected on trees fogged for the first time varied considerably between 7 and 238, representing between 0.72% and 3.4% of all fogged arthropods. The proportion of nymphs within primary fogging samples fluctuated between 80 and 100% (mean 82.94 ± 19.59). This pattern was independent of the month of fogging and showed no seasonality. In the stem eclectors, 787 specimens were collected, and the proportion of nymphs was significantly higher than in the fogging samples (mean 96.9 ± 5.28, Mann Whitney U-test, $P < 0.001$). Table 1 compares the higher taxonomic composition of fogged Orthoptera versus those caught by eclector traps, ranked by the number of nymphs. Adults occurred only sporadically in the stem eclectors. Highest in abundance in both fogging and eclector samples were the Podoscirtinae (hard-footed bush crickets). In the fogging samples, Mogoplistinae (scaly crickets) followed in second place, but had by far the highest number of adults. The differences between larval:adult proportions of the dominant Podoscirtinae and Mogoplistinae point to differences in the life cycle; however we cannot exclude the possibility that this result was influenced by differences in flight capability (adult Podoscirtinae are fully winged flying species, while in Mogoplistinae the wings are reduced or absent and they are unable to fly). In the eclector traps the Mogoplistinae dropped to rank six, while the omnivorous Pteroplistinae rose to the second rank. Pteroplistinae first-instar nymphs formed groups ranging between 7 and 25 individuals, suggesting that nymphs climbed up the stems immediately after hatching in the soil, lower vegetation, or from crevices in the bark. In contrast, the low numbers of Mogoplistinae nymphs in the eclectors indicate a preference for the canopy throughout their life. All other taxa were represented by only a few individuals or singletons in each sample. A remarkable general feature was the low percentage of short-horned grasshoppers (Caelifera) which were represented by only 32 nymphs in the fogging samples. They occurred as single individuals or in small groups of up to four (Acridoidea) or ten individuals (Eumastacoidea). Tetrigoidea always occurred as singletons; three of the specimens found in stem eclectors were adults.

For the Ensifera, Table 2 compares the number of adult species and their taxonomic status in the fogging samples with those collected by hand and by light-traps. A total of 127 morphospecies were differentiated, of which 85 were new; 32% (41/127) of all species were obtained by fogging only. Within the fogging samples the proportion of new species was 98%, while "only" 49% of species collected with conventional methods were new. Only 8% (6/76) of tettigoniid and 2% (1/44) of grylloid species were collected both by fogging and conventional methods. Such a small overlap suggests the existence of a separate canopy fauna. "Canopy" taxa ('only fogging') which provided most new species were Pseudophyllinae, Meconematinae, Gryllacrididae, Podoscirtinae, and Mogoplistinae. Most other groups were collected predominantly by conventional methods, indicating a preference for lower forest strata.

TABLE 1. Ranks of Orthopteran groups according to the number of nymphs collected by fogging and with stem eclector traps. Guild assessment according to feeding habits: H = herbivorous, O = omnivorous, P = predators.

	Fogging					Stem-eclectors				
Rank Group	Guild	Total	Adults	% Adults	Nymphs	Total	Adults	% Adults	Nymphs	Rank
1 Podoscirtinae	H	826	40	4,8	786	326	2	0,6	324	1
2 Mogoplistinae	O	545	161	29,5	384	35	5	14,3	30	6
3 Meconematinae	P	318	34	10,7	284	75	–	–	75	4
4 Trigoniinae	H?	161	22	13,7	139	38	–	–	38	5
5 Gryllacridoidea	O	171	11	6,4	160	78	2	2,6	76	3
6 Pteroplistinae	O	101	4	4,0	97	186	1	0,5	185	2
7 Phaneropterinae	H	84	14	16,7	70	29	–	–	29	7
8 Pseudophyllinae	H	57	7	12,3	50	11	1	9,1	10	8
9 Conocephalinae	O	26	–	–	26	1	–	–	1	9
10 Lipotactinae	P	3	2	66,7	1	0	–	–	–	–
11 Caelifera	H	32	–	–	32	8	3	37,5	5	–
Total		2324	295		2029	787	14		773	

TABLE 2. Species numbers and taxonomic status of adult Ensifera collected by fogging and conventional techniques (hand collected and light-traps).

	Only fogging		Only hand & light sampling		Collected with both methods		Total	
	Total	New	Total	New	Total	New	Total	New
TETTIGONIOIDEA								
Phaneropterinae	2	2	20	13	4	4	26	19
Pseudophyllinae	4	3	16	6	0	0	20	9
Meconematinae	5	5	1	1	0	0	6	6
Mecopodinae	0	0	4	0	0	0	4	0
Conocephalinae-Conocephalini	0	0	2	0	0	0	2	0
Conocephalinae-Agraecini	0	0	12	7	1	0	13	7
Conocephalinae-Copiphorini	0	0	2	0	0	0	2	0
Hexacentrinae	0	0	1	0	0	0	1	0
Lipotactinae	0	0	1	1	1	1	2	2
Sum	11	10	59	28	6	5	76	43
% new species		91%		48%		83%		57%
GRYLLOIDEA								
Podoscirtinae	12	12	3	3	1	1	16	16
Pteroplistinae	2	2	2	2	0	0	4	4
Mogoplistinae	5	5	0	0	0	0	5	5
Trigoniinae	4	4	0	0	0	0	4	4
Nemobiinae	1	1	3	0	0	0	4	1
Gryllinae	0	0	2	1	0	0	2	1
Itarinae	0	0	4	2	0	0	4	2
Eneopterinae	0	0	1	0	0	0	1	0
Oecanthidae	0	0	1	0	0	0	1	0
Myrmecophilidae	0	0	1	1	0	0	1	1
Gryllotalpidae	0	0	2	1	0	0	2	1
Sum	24	24	19	10	1	1	44	35
% new species		100%		53%		100%		80%
GRYLLACRIDIDAE	6	6	0	0	1	1	7	7
% new species		100%				100%		100%
TOTAL	41	40	78	38	8	7	127	85
% new species		98%		49%		88%		67%

Composition and recolonization dynamics of the Orthopteran fauna. The rank-abundance plot of all foggings (Fig. 1) gives the typical pattern of species distribution known from tropical lowland rain forests, with almost all species being rare as adults. The majority of all species were singletons (49%) and only three species (all Mogoplistinae) were found with more than ten individuals; *Ornebius marginatus* represented by 67 individuals, *O. flori* by 48, and *O. rubidus* by 11 individuals. Even the more abundant species did not aggregate on particular trees, occurring on almost every tree with some individuals irrespective of the tree species (Fig. 1). The steep increase of the Shinozaki curves (Fig. 2) and the low Soerensen indices (Table 3) demonstrate that species overlap among individual trees was low, and that overall sampling effort was not sufficient to represent or estimate total species number at the regional or even local

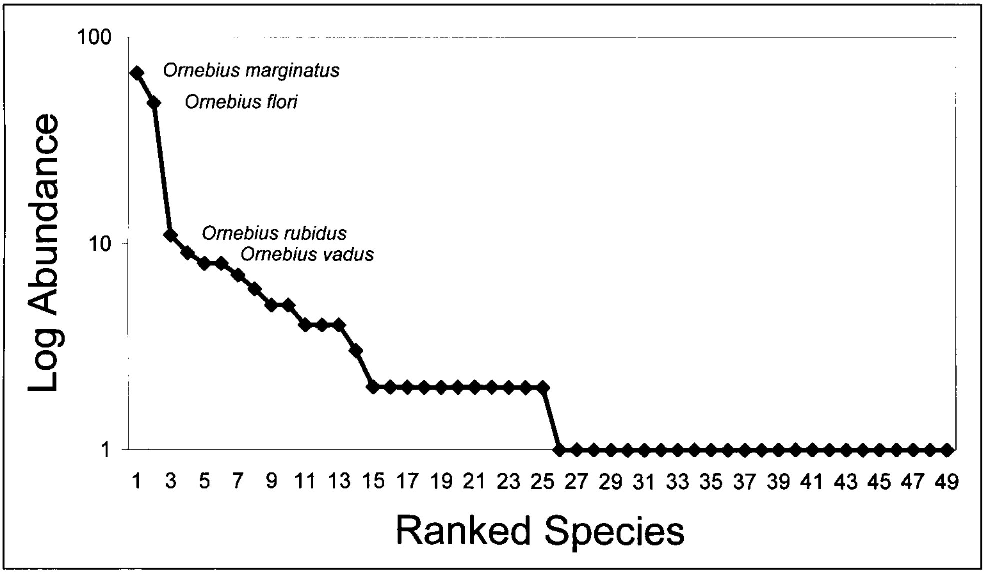

FIG. 1. Rank-abundance curve plotted for the Orthoptera of all fogs.

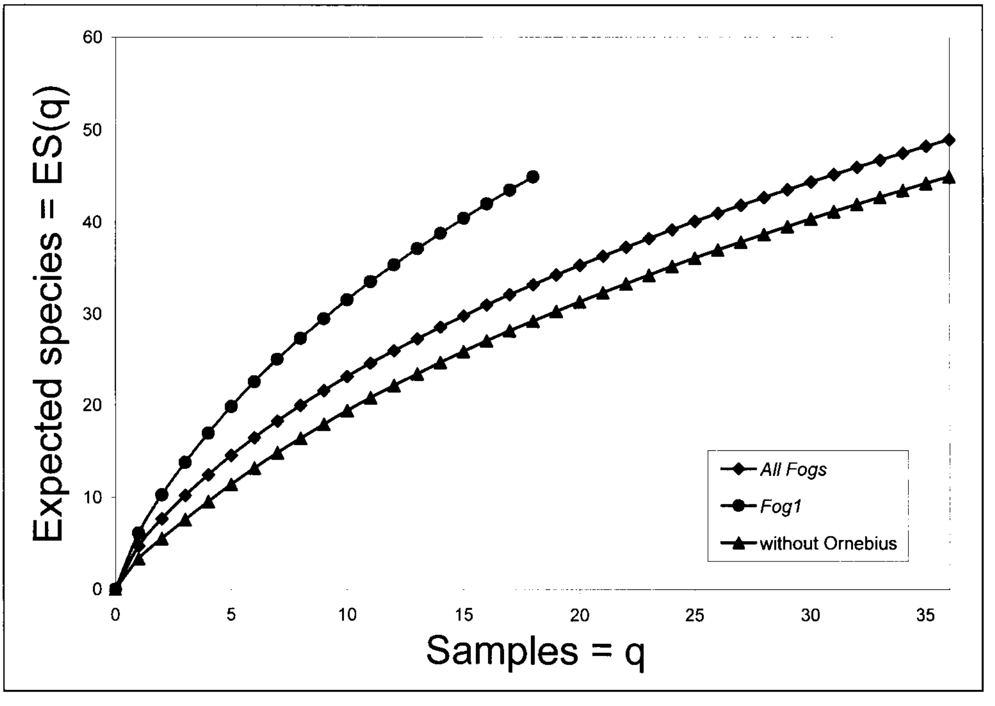

FIG. 2. Shinozaki curves computed for primary fogged trees, for all foggings, and for all foggings excluding the most numerous *Ornebius* spp. q = number of discrete samples (fogged trees), ES(q) = expected number of species in q samples.

TABLE 3. Mean beta-diversities between the fogged trees expressed by the Soerensen index. Standard deviations in brackets.

Tree species		Soerensen
A. lagenocarpa	(n =10)	0.16 (0.17)
A. subcaudata	(n =5)	0.16 (0.14)
X. affine	(n = 4)	0.28 (0.34)
All trees		0.20 (0.21)

scale. The Shinozaki curves are far from reaching an asymptote, independently of whether all fogging samples (primary- and re-foggings), only primary foggings, or only samples without the most common *Ornebius* spp. were included in the calculation.

Adding species captured in the re-fogging experiments always resulted in a larger number of new species, without changing the steepness of the curve.

Fig. 3 shows the standardized numbers of Orthopterans from the trees fogged for the first time and those re-fogged at various intervals of time. The number of individuals within daily re-foggings was significantly lower than those of the primary fogged trees (Mann-Whitney U-test, P = 0.007) and also than those of the re-foggings after 6 months (M-W U-test, P = 0.002). The number of individuals caught in the daily samplings was not significantly different from that obtained by weekly sampling due to an outlier, and the same was true for all Orthopterans collected weekly and in comparison to those collected after more than six months. However, because of the few samples involved this lack of significance should not be taken too seriously. The proportion of nymphs was equally high in trees fogged for the first time (87%) and in those re-fogged after one week and after six months, but lower in samples derived from daily re-foggings (66%).

For all foggings the majority of specimens captured belonged to five subfamilies (see Fig. 4a), which together contributed between 76% of all specimens in the daily samples and 90% in the samples taken after six months. Only the Podoscirtinae and Meconematinae showed significant variation in numbers under different fogging regimes (for the Podoscirtinae: K-W-Anova, χ^2 = 11.34, P = 0.010; for the Meconematinae: χ^2 = 9.46, P = 0.024) (the 'Unknown' group was not considered). A similar pattern emerged when the composition of the feeding guilds between the various times of foggings were compared (Fig. 4b). Guild classification corresponds to that of Table 1 and distinguishes omnivores, herbivores, and predators. Only predators in the daily samples differed significantly from the other foggings (K-W-Anova, χ^2 = 9.39, P = 0.024), caused by an increase in Meconematidae which were the fastest newcomers (see Fig.4).

DISCUSSION

Characterization of Orthopteran communities. Arthropod diversity in tropical rainforests, and in particular in the canopy, has received much attention during the last decade, but analysis has been mainly based on Coleoptera and Formicidae (e.g., Erwin 1982, Stork 1991, Basset 1996, Stork *et al.* 1997, Linsenmair *et al.* 2001). We here present data on the Orthopteran fauna of three Bornean lowland rain forest tree species, considering both adults and nymphs. The constant high percentage of nymphs within each tree crown community was independent of the month of fogging and indicates continuous reproduction in most species. Despite quite a substantial sampling effort, relatively few adult specimens (representing only

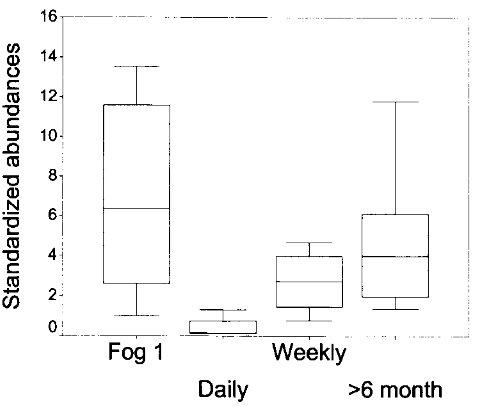

FIG. 3. Mean numbers of Orthopteran individuals calculated for a crown projection of 1m² and a leaf cover of 100%. Primary foggings (n = 19) are compared with re-foggings after different intervals of time. Daily: four re-foggings of a single tree on four consecutive days; Weekly: re-foggings of four trees after one week; > 6 month: re-foggings of ten *Aporusa*-trees after six months.

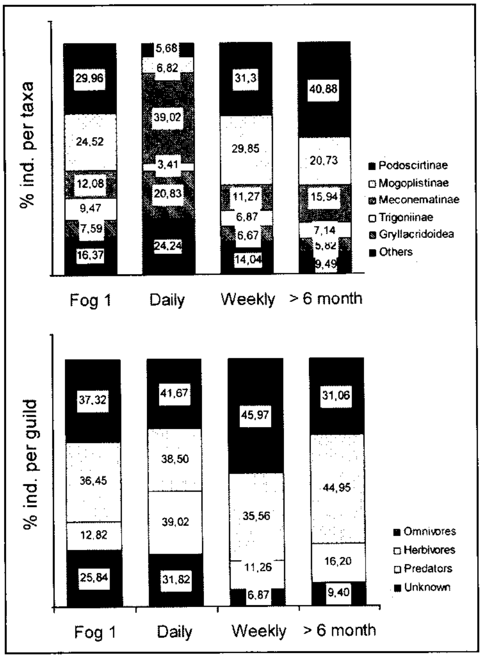

FIG. 4. Relative proportion of a) Orthopteran subfamily- and b) feeding guild composition in foggings carried out after different periods of time. Labeling of fogging categories as in Fig. 3.

13% of all specimens) were collected and assigned to morphospecies. Our sampling revealed surprising species richness: all fogged Grylloidea and 91% of Tettigonioidea belonged to hitherto undescribed taxa. Even conventional collection methods (light-trapping, hand collecting, and stem eclectors) revealed 49% of species as new.

As is typical for tropical insect faunas, the majority of Orthoptera species occurred in small numbers and sampling effort was much too small to represent local species diversity or even to assess the necessary further sampling effort required for reliable estimates. The highest ranks in species richness and abundance among fogged species – considering adults as well as nymphs – were occupied by two cricket subfamilies – Podoscirtinae and Mogoplistinae. However, only two species of Mogoplistinae (genus *Ornebius*), which are generalist feeders, occurred on all tree individuals. These species were lacking in the stem eclectors, have not been sampled from the ground (Riede unpublished), and were new to science (Ingrisch 1998), thus indicating that they are confined to the canopy. Recent studies reveal that at least some species of the Podoscirtinae do not need to go to the soil in any part of their life cycle, for example for egg deposition (Ingrisch 1997). However, for most species observations on life habits are lacking. The fact that we also collected juveniles of all instars of these species by fogging suggest they are really canopy specialists.

Our data do not allow us to draw any conclusions about the existence of a tree-species-specific Orthopteran community. However, host tree adaptation might emerge if sampling effort were significantly extended and if nymphs, which belong to the same feeding guilds as adults, could be included in the analysis. However, an adequate consideration of nymphs would require comprehensive taxonomic and autecological studies. A preliminary analysis of a further 39 foggings in the mature forests, which include ten additional tree species, does not show a change in the pattern described above (Floren unpublished). Trees in general seem to provide similarly favorable conditions for omnivorous species, and no differences in habitats – like the presence of epiphylls, stem cavities, aggregations of detritus, etc. – were found (Floren & Linsenmair 1998a). The failure to identify a tree-species-specific Orthopteran community corresponds with the findings for other taxa, such as Coleoptera (e.g., Floren & Linsenmair 1998b, Wagner 1999), Ichneumonidae (Horstmann *et al.* 1999), or Formicidae (Floren & Linsenmair 1997, 2000), but see the study by Amédégnato (1997) on Acrididae of an Amazonian rain forest. The question of how many arthropod species are tree specialists is still intensively discussed (Erwin 1982, Basset 1996, Basset *et al.* 1996, Mawdsley & S

tork 1997, Oedegaard 2000). In addition, the lack of the existence of a tree-specific community is supported by our result that Orthoptera were obviously sampled at random from a large species pool: neither the taxonomic nor the guild composition of Orthopteran communities had changed significantly in the re-fogging samples. Orthoptera colonize trees rather slowly compared to Coleoptera and Diptera, which can reach original abundances already after one day (Floren & Linsenmair 1998a). While the total number of Orthoptera dropped significantly in the daily foggings, the proportion of adults and nymphs did not change. The predatory Meconematinae were the fastest colonizers. However, relative proportions showed no significant differences from the original conditions already after one week, indicating that most specimens enter tree crowns from neighboring trees according to their frequency in the species pool, without tree-species-specific features being important. From our data we were not able to distinguish either pioneer or climax species, such as were identified by Amédégnato & Descamps (1980) in large forest gaps and anthropogenic clearings.

We compared our results with fogged material from Sulawesi (see Knight & Holloway 1990). As in our investigation, Podoscirtinae and Mogoplistinae were dominant there. Podoscirtinae included almost twice as many larvae as Mogoplistinae, but Mogoplistinae were more numerous as adults. There were four species of Mogoplistinae (probably undescribed) which belong to the genera *Ectatoderus* and *Ornebius* and which are specifically different from the species occurring on Mt. Kinabalu. This might indicate a high degree of endemism for the fauna of the region of Mount Kinabalu, which is a center of diversity in SE Asia (Ashton 1989, Myers *et al.* 2000).

The extreme rarity of short-horned grasshoppers (Caelifera) in our samples was surprising and is in contrast to Amazonian and Costa Rican rain forests (Roberts 1973, Descamps 1981, Riede 1993, Amédégnato 1997). Arboreal grasshoppers are characterized by a vivid coloration, stout legs and body form, and protuberant eyes, summarized as the "dendrophilous" life form by Descamps (1976, 1981). Many species are brachypterous or apterous. Some species have developed endophytic and epiphytic egg-laying strategies, which would allow them to spend their whole life cycle – from egg to adult – in the canopy (Amédégnato 1997). An analysis of museum specimens shows that the SE-Asian grasshopper fauna contains similar dendrophilous species which are, however, very rare (Riede 1993). This is corroborated by fogging studies by Stork (1991) in Brunei, and the additional 39 foggings of 10 tree species from seven families in Kinabalu Park (Floren unpublished). The rarity of Caelifera does not seem to be a sampling artifact. Among the possible causes of this rarity, Riede (1993) discusses higher predation pressure and canopy structure as well as food plant availability and palatability. However, we must admit that Caeliferan scarcity in SE-Asian rainforests is still an enigma.

Differences between holometabolous and hemimetabolous arthropods that affect community composition. To date, most analyses of "canopy faunas" have been limited to adult holometabolic insects. Already in our first fogging samples we recognized that nymphs of holometabolous species were almost completely lacking in the trees (Floren & Linsenmair 1997, 1998a, b, 1999). Their absence from the tree crowns was confirmed by additional hand collecting, close observations in the trees (Riede, unpublished), and further foggings. In contrast, nymphs of hemimetabolous taxa, especially of the numerically dominant Hemiptera and Orthopteroidea sensu latu, are found regularly and in high abundances, always outnumbering adults. This difference can be explained by the high predation pressure of the ants, that dominate all trees and patrol in the canopy regularly (Floren submitted). Experimental feeding with caterpillars demonstrates the high predation pressure exerted by canopy ants, most of which attacked less mobile prey. By contrast, the nymphs of hemimetabolous groups are highly mobile and therefore able to escape from predatory ants. Similarly, eggs have to be protected by endophytic or subterranean oviposition. Nymphs which hatch in the soil or from the lower vegetation layers could then climb up to the canopy to complete their life cycle. This might be an explanation for the higher percentage of nymphs observed in our eclector samples compared with the fogging samples and points to the importance of tree trunks as routes to reach the canopy. On the other hand, in several tettigoniid subfamilies (Phaneropterinae, Pseudophyllinae, Meconematinae) endophytic oviposition prevails, and the same could be true for the cricket subfamily Podoscirtinae, which was the dominant taxon in our investigations. This could mean that many of the arboreal species complete their life cycles in the canopy. However, given the present state of knowledge these interpretations must remain speculative, since biological information on tropical Ensifera is generally scarce (e.g., Bailey & Rentz 1990).

ACKNOWLEDGMENTS

We are grateful to the Director of Sabah Parks, Datuk Ali Lamri, for authorization of our research, and to park staff for generous support. The fogged material from Sulawesi was kindly lent by Judith Marshall (Natural History Museum London). We thank C.H.F. Rowell for critical comments on the manuscript. This study was supported by the German Research Council (DFG), Li 150/13 1–4.

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