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NON-EQUILIBRIUM COMMUNITIES OF COLEOPTERA IN TREES IN A LOWLAND RAIN FOREST OF BORNEO

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Abstract. An improved method of canopy fogging, which allowed tree-specific sampling, was used to investigate the composition, structure, and recolonization dynamics of arboreal arthropod communities in a south-east Asian lowland rain forest. The aim of our investigations was to assess whether arthropod communities exhibit mainly equilibrium or non-equilibrium properties. In this paper we present data on the Coleoptera. The relative proportion of Coleopteta was always around 5% despite much variation in total arthropod abundance (1400 to 10,600 arthropods on the first 19 trees fogged). At the morphospecies level, all Coleoptera communities were characterized by high alpha and beta-diversity and very few species overlapped between trees. 96% of species comprised less than 10 individuals and 60% were singletons. Since indications of equilibrium and non-equilibrium community structure can be derived from the analysis of recolonization, refogging experiments were conducted after differing intervals of time. With one exception the Coleoptera distribution patterns of the trees fogged initially were also found in the samples of the refogging experiments. Even after pooling the beetles from all foggings, the total sample consisted mainly of rare species. The described species abundance patterns are not distinguishable from random distributions and beetle communities are very clearly examples of communities in non-equilibrium. *Accepted 10 June 1998.*

Key words: Borneo, lowland rain forest, fogging, refogging, Coleoptera, non-equilibrium communities, species complexes.

INTRODUCTION

Coleoptera are probably the most species-rich taxon on earth and represent almost 40% of all arthropods (May 1994). As such, they are often used as a target group to characterize terrestrial habitats or communities. This is especially true for tropical ecosystems (Erwin 1982; Stork 1987; Allison *et al.* 1993, 1997; Basset 1996; Mawdsley & Stork 1997; Hammond *et al.* 1997; Wagner 1997). Species richness reaches extreme dimensions here, with the consequence that today it is still impossible to quantify the diversity of tropical Coleoptera at the species level. Nevertheless, many ecologically important conclusions were and still are drawn from those investigations. Probably the best known example is Erwin's speculative calculation of thirty million insect species living on tropical trees alone (Erwin 1982). The fact that Erwin's estimation is still controversially discussed shows how small the data basis for such calculations is and how disputed the assumptions are on which they rely (e.g., Stork 1993, May 1994, Basset *et al.* 1996, Hammond et al. 1997). This is mainly a consequence of the phenomenon that most species are extremely rare in lowland rain forests, while highly abundant species, which are common in the temperate systems (e.g., Nielson 1975, Southwood *et al.* 1982, Wagner 1996), are generally missing (compare Table 6). Such a pattern makes it very difficult to infer essential ecological traits of species, like whether they are specialists or generalists, or whether they are widely or narrowly distributed, or whether they are efficient or poor dispersers.

We wanted to make some contribution to narrowing these substantial gaps in our basic knowledge by studying the mechanisms structuring the coleopteran communities living within the tree crowns of a few selected tree species. Thus, we aimed at finding patterns in beetle communities on the species level which could give us clues to the underlying determinants. The question was whether we would be able to find tree-specific and repeatable community patterns that would then point to the existence of deterministically structured communities in equilibrium or, alternatively, would we find communities of such variability that non-equilibrium processes are more likely as structuring forces (see Wiens 1984, Floren & Linsenmair 1997). We chose trees of three species showing a high degree of similarity in tree structure and habitat conditions, and sampled

their arthropod communities tree-specifically using an improved method of canopy fogging. Community reorganization on fogged trees was investigated through refogging experiments conducted after differing intervals of time. The analysis of these experiments should indicate whether, and if at all, recolonization followed a deterministic dynamic. This should be identifiable through the successional dynamic as well as through the occurrence of typical pioneer and climax species (e.g., Kikkawa & Anderson 1986).

METHODS

This study was carried out in the lowland forest of Kinabalu National Park, substation Poring Hot Spring, on Borneo, Sabah, Malaysia (6°5'N, 116°33' E). Several individuals of three tree species were selected, 10 *Aporusa lagenocarpa*, five *Aporusa subcaudata* (Euphorbiaceae), and four *Xantophyllum affine* (Polygalaceae). All three species are trees of the lower stratum of primary forests reaching less than 30 meters, while their crown diameter rarely exceeds 10 m. During the fogging phase none of the trees showed large leaf flushes, on the other hand smaller leaf flushes were occasionally observed. However, as this did not influence the composition of the arthropod communities in a recognizable way we did not quantify this.

In order to sample tree-specific arthropod communities we used selective canopy fogging (Floren & Linsenmair 1997, a photographic presentation is given in Floren & Linsenmair 1998). All arthropods knocked down from trees of the higher canopy were excluded by stretching out a 100 m^2 cotton roof over the top of the crown of the fogged tree. Many funnels were positioned beneath each treated tree so that 80 to 90% of the ground under the tree was covered. Fogging was conducted at 06:00 h in the morning when there was little wind drift, and always applied inside the tree crown to guarantee that all parts of the crown were fogged evenly. A 2% concentration of natural pyrethrum insecticide (dissolved in a highly refined white oil, ESSOBAYOL 82) was used which is highly specific to arthropods, and breaks down in minutes in direct sunlight. The arthropods that dropped into the funnels during the two hours following fogging were stored in 80% alcohol and sorted in the laboratory. A total of 40 such samplings were conducted over 1992 and 1993. Of the 19 trees initially fogged, 10 were refogged after six months, six at weekly intervals, and one was fogged five times on consecutive days.

The Coleoptera groups used for evaluation. We studied only phytophagous beetles (mainly Chrysomelidae and Curculionidae) because we expected to find repeated tree-specific species associations, if at all, among the oligophagous or monophagous specialists of this guild. The Coleoptera were categorized on the morphospecies level because of the insufficient taxonomic knowledge of most groups. Most species were clearly different and could easily be separated from each other. In several cases beetles were analyzed by specialists through the preparation of genitalia. In this work Sharon Shute and Martin Brendell from the Natural History Museum in London were of great help.

Statistical analysis. Community structure was analyzed by computing alpha and beta-diversity indices and rarefaction statistic. Formulas are discussed in Magurran (1988) and Floren & Linsenmair (1997). Alpha-diversities included species number, Shannon's index, evenness, and Simpson's index. We calculated Whittaker's beta-index to estimate the size differences between the regional and the smaller average local species pool. Soerensen's index was used as a measure of relative similarity in species composition between two communities. In order to obtain an average beta-diversity value of more than two subsamples the mean value of all possible combinations was computed. For example, the mean beta-diversity of all 10 individuals of *Aporusa lagenocarpa* results from $(n^2-n)/2 = 45$ combinations.

For all samples, rarefaction accumulation curves were computed whose shapes depend on the species-abundance distributions. These curves are directly comparable with each other. All samples were regarded as being independent in a statistical way since there was no indication that beetles were aggregated on the trees, which would led to an overestimation of species richness (Hurlbert 1971, Achtziger *et al.* 1992). Applying rarefaction methodology to species presence-absence data provides information about the overall completeness of the sampling effort (Shinozaki 1963, Smith *et al.* 1979). All additional attempts to characterize the Coleoptera communities, for example by distribution models or the calculation of species associations, did not lead to any significant results (Floren 1996, see discussion).

RESULTS

All 40 foggings yielded 8856 Coleoptera of 77 families, and so far 4705 individuals have been allotted to 1183 morphospecies. After reconfirmation by specialists we estimate the total number of species to be about 2000. Within the whole sample, Chrysomelidae represented the largest group with 23.9% (2117 individuals) and 485 species, followed by Curculionidae, which contributed 11.1% (983 individuals) and 257 species, and Staphylinidae with 10.9% (965 individuals, species numbers not yet determined). While these groups were collected from all trees, abundances of the remaining 74 families showed large fluctuations between trees. Most of the species collected were highly mobile, while less mobile species and larvae were almost totally absent. Evidence for high mobility comes from morphology (all were able to fly), refogging experiments, and tests of the efficiency of the fogging (Floren & Linsenmair 1997, see discussion below).

The Coleoptera communities of the trees fogged initially. From all 19 trees fogged for the first time, 2168 beetles were sampled, that is 24.5% of all the Coleoptera. Among these were 1063 beetles considered to be phytophagous, which were sorted to 688 morphospecies. Chrysomelidae formed the largest group with 304 morphospecies (44.2%), followed by Curculionidae with 172 morphospecies (25.0%). Thus, these two phytophagous groups provided almost 70% of all species considered in this evaluation.

409 species (59.4%) were collected with only one individual, and 659 species (95.8%) with less than 10 individuals. Two species of Alticinae (Chrysomelidae) were the most abundant species with 119 and 87 individuals respectively. Of all beetle species sampled from each tree, on average 75.0% (SD 7.3) were singletons while only 1.1% (SD 1.6) were represented by more than 10 individuals. This distribution was characteristic for each single community as well as for all pooled Coleoptera (Fig. 1).

The distribution of the most abundant species is shown in Table 1. It confirms the special importance of Chrysomelidae, which contained, with only one exception, all of the 12 most abundant species. It further shows that the most abundant species were either found in relatively large numbers on few trees or in low numbers in many trees. No single species

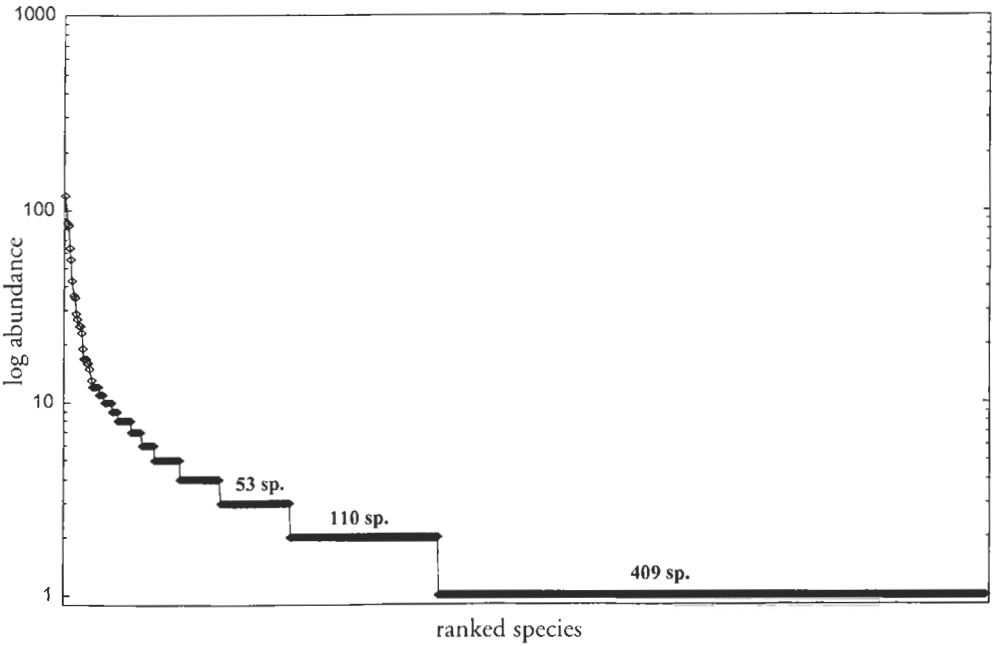

FIG. 1. Species abundance distribution of the phytophagous Coleoptera of all 19 trees fogged for the first time. The figure is based on 1063 individuals sorted to 688 morphospecies.

TABLE 1. All species of Coleoptera found with more than 20 individuals on the 19 initially fogged trees. Total abun. = specimens in all samples, max. abun. = maximal abundance per tree, num. of trees = number of trees in which the species was found.

Taxa			total abun.	max. abun.	num. of trees
Chrysomelidae	Alticinae	sp. 1	119	90	2
Chrysomelidae	Alticinae	sp. 2	87	23	15
Chrysomelidae	Galerucinae	sp. 3	84	68	2
Chrysomelidae	Eumolpinae	sp. 4	64	43	8
Chrysomelidae	Alticinae	sp. 5	56	47	5
Curculionidae	Cryptorhynchinae	sp. 6	43	13	11
Chrysomelidae	Eumolpinae	sp. 7	36	10	9
Chrysomelidae	Alticinae	sp. 8	36	25	5
Chrysomelidae	Eumolpinae	sp. 9	29	24	4
Chrysomelidae	Galerucinae	sp. 10	27	8	8
Chrysomelidae	Galerucinae	sp. 11	25	5	13
Chrysomelidae	Galerucinae	sp. 12	25	7	6

TABLE 2. Alpha-diversities of the phytophagous Coleoptera communities of all 19 primarily fogged trees. A.l. = *Aporusa lagenocarpa*, A.s. = *Aporusa subcaudata*, X.a. = *Xantophyllum affine*. S = Species number, Abun. = abundancies, Shan. = Shannon index, Even. = evenness, Simp. = Simpson index.

Tree Nr.	(S)	Abun.	Shan.	Even.	Simp.
A.l. 5	22	41	2.66	0.86	0.91
15	45	112	3.09	0.81	0.91
52	77	111	4.12	0.95	0.99
57	7	9	1.89	0.97	0.94
62	39	39	3.35	0.97	0.98
70	64	126	3.84	0.92	0.98
71	48	68	3.70	0.97	0.98
72	78	186	3.48	0.80	0.92
73	80	163	4.03	0.92	0.98
74	87	184	4.00	0.89	0.97
A.s. 8	32	49	3.23	0.93	0.97
9	118	381	3.49	0.73	0.91
10	26	37	3.13	0.96	0.98
50	52	82	3.64	0.92	0.97
51	166	376	4.52	0.88	0.98
X.a. 4	20	23	2.94	0.97	0.99
5	13	15	2.52	0.98	0.98
11	50	75	3.66	0.93	0.97
12	46	91	3.32	0.87	0.95

occurred on all 19 trees. Only one individual tree, *Aporusa* #8, was flowering during the study but without having any noticeable effect on the composition of its beetle community.

The alpha-diversities of the Coleoptera communities. The alpha-diversity and evenness values of all beetle communities (Table 2) demonstrate that there was hardly any difference between trees with regard to species richness and abundance distribution. 166 species, most belonging to the Eumolpinae (Chrysomelidae), were collected from the crown of *A. subcaudata* #51, thus representing the richest phytophagous beetle community found in all trees we investigated in this study. Why the samples of *A. lagenocarpa* #57 and *X. affine* #5 had so few species and such low diversity values is not understood. We were not able to recognize any striking difference in any of the tree properties or change of external conditions during these foggings which might have been responsible for these deviations.

One consequence of the many rare species is that the rarefaction curves correspond to nearly straight lines (Fig. 2). This was true for all beetle communities from all individual trees, no matter how many individuals they consisted of.

Computing the rarefaction curves for all pooled samples gives an impression of the regional diversity. Against that, the Shinozaki curve, which is based on

presence-absence data only, is a graphical illustration of the beta-diversity. The steepness of both curves confirms the large discrepancy between the number of species sampled and the actual dimension of the species pool, and shows that these data are insufficient for estimating the size of the regional species pool or for predicting to what extent sample size would have to be increased to reach species saturation.

The beta-diversities of the Coleoptera communities. As already indicated by the Shinozaki curve, species overlap between trees was very low. How little the beetle communities corresponded in species composition is shown further by the beta-diversity indices (Table 3). Comparing individual trees within the same species, as well as between the three tree species, always resulted in very high Whittaker and low Soerensen values respectively, demonstrating that every community was an almost unique species assembly.

The refogging experiments. Independent of the time between the initial foggings and the refoggings performed at weekly intervals or six month later, the results were indistinguishable from those of the primary experiments. Once again the Chrysomelidae, Curculionidae, and Staphylinidae were the most abundant Coleoptera. The many rare species hardly showed any overlap between trees so that the values of the alpha- and beta-diversities remained at the same high level. How quickly beetles were able to colonize an 'empty' tree crown became apparent from the results of the five foggings of *Aporusa* #73 conducted on consecutive days (Table 4).

The total number of beetles decreased continuously until the fifth fogging but, surprisingly, increased after the following fog which was as rich in beetles as the first sample. We cannot explain this increase, but it was not caused by any evident change

TABLE 3. Mean beta-diversities of each index of all possible combinations for all tree species. Standard deviations in brackets.

Tree species		Whittaker	Sørensen
A. lagenocarpa	(n=10)	0.90 (0.07)	0.10 (0.06)
A. subcaudata	(n= 5)	0.90 (0.05)	0.10 (0.05)
X. affinae	(n= 4)	0.94 (0.04)	0.06 (0.05)

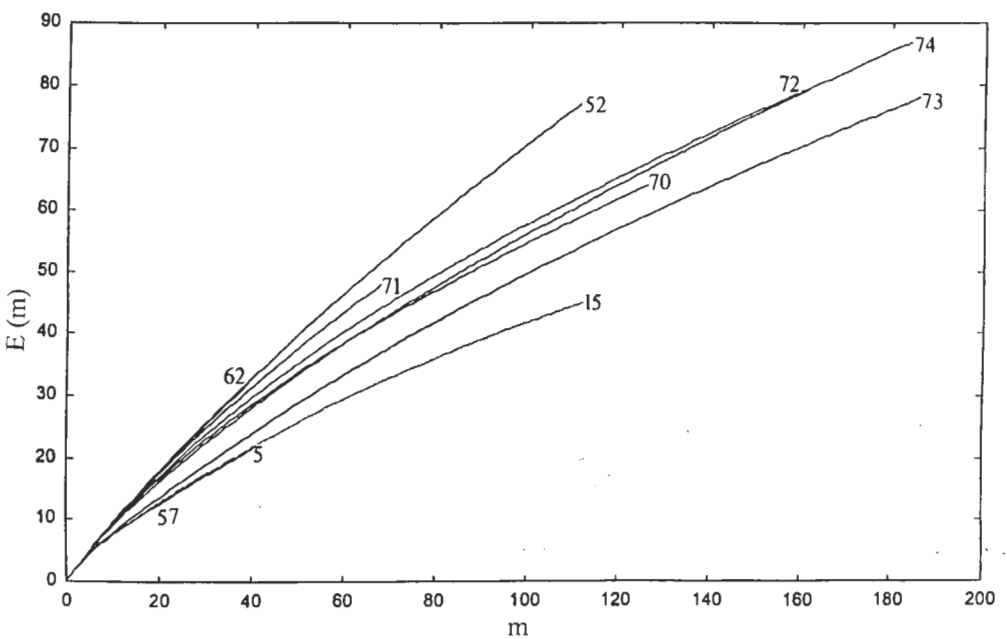

FIG. 2. Rarefaction curves of the Coleoptera communities of all 19 initially fogged *Aporusa lagenocarpa* trees. E(m) = Expected number of species in m subsamples.

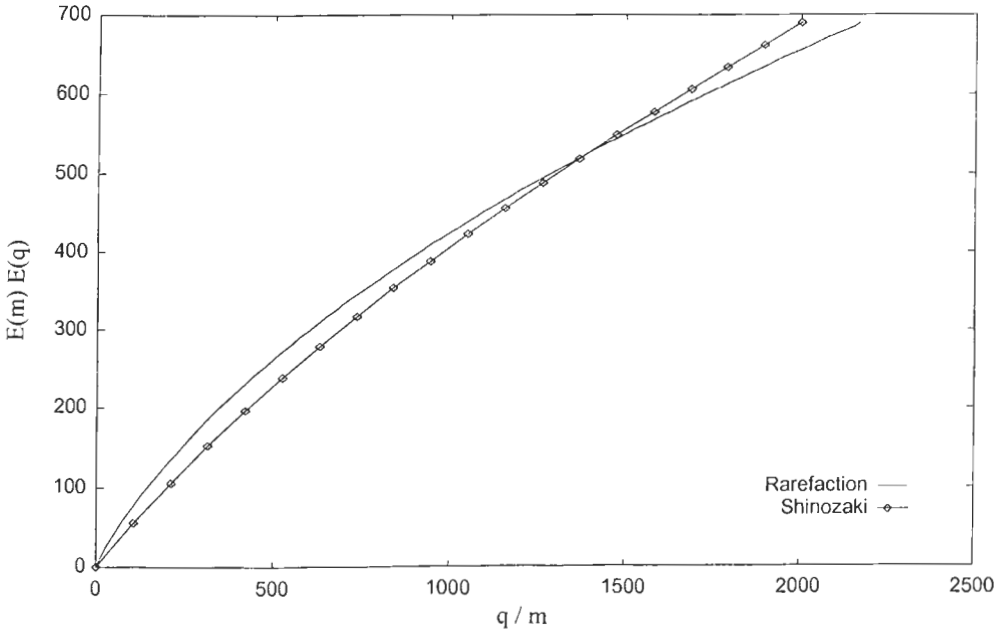

FIG. 3. Rarefaction and Shinozaki curves of the Coleoptera communities of all initially fogged trees. E(m) = Expected number of species in m subsamples. E(q) = Expected number of species in q discrete samples.

in the external conditions, for example, which remained stable during all five consecutive foggings. This tree in particular was interesting because Malachiidae as well as Mordellidae were found in larger quantities in every sample than in all others. Of all 228 identified species from all consecutive daily foggings, 172 (75.4%) occurred in one sample only, and 142 (62.3%) were found as singletons. Only four species were represented by more than 10 individuals in a single fogging sample. A malachiid beetle was the most common species with 54 individuals in fog 5. With one exception, all Malachiidae were Calphorinae (genus *Carphurus*), while only one species belonged to the intercontinental genus *Balanophurus* (Evers, pers. comm.). Mordellidae have not yet been identified to morphospecies.

A surprising result was produced by refogging *Aporusa* #51 after nine days. Here, the number of beetles found initially, 531 individuals and 166 species, had more than tripled to 1854 individuals and 288 species. After the following refog 10 days later, the number of specimens was found to lie distinctly

TABLE 4. Absolute numbers and relative proportions of the five commonest families of Coleoptera in relation to the total number of beetles from each of five daily consecutive foggings of *Aporusa* #73.

	Fog 1		Fog 2		Fog 3		Fog 4		Fog 5	
	Ind.	%	Ind.	%	Ind.	%	Ind.	%	Ind.	%
Beetles per Fog	326		175		126		62		314	
Chrysomelidae	78	23.9	49	28.0	32	25.4	11	17.7	50	5.9
Curculionidae	52	15.9	9	5.1	5	4.0	4	6.5	14	4.5
Staphylinidae	36	11.0	17	9.7	12	9.5	9	14.5	23	7.3
Malachiidae	52	15.9	9	5.1	4	3.2	3	4.8	60	19.1
Mordellidae	36	11.0	8	4.6	11	8.7	0	0.0	24	7.6

below the second and the first value, with 179 individuals and 56 species. Strikingly, almost 32% of all beetles from the second fogging were found to belong to three large species groups (Table 5). All were morphologically very similar and could be separated only by dissection of genitalia. Including some smaller groups, almost 45% of all specimens of this sample were found in such species groups. Only in these aggregations, and confined to this fogging experiment, did we find single species in relatively high abundances, all of which remained rare in the other fogging samples. The largest of such aggregations were detected within the genera *Nodina* and *Monolepta* (Eumolpinae, Chrysomelidae), *Otiorhynchus* (Otiorhynchinae, Curculionidae), and *Formicomus* (Anthicidae). Alerted by this result, we also detected such associations in further samples but to a much lower degree. They consisted of up to 10 species that occurred exclusively in one tree and were found within the Dascillidae, Scirtidae, Erotylidae, Nitidulidae, Othniidae, Pselaphidae, Sphindidae, Scaphidiidae, and Merophysidae. We call these spatially confined occurrences of genera-specific species associations species complexes. They might indicate an as yet unrecognized phenomenon of species organization in the tropics as discussed below.

TABLE 5. Species abundance distributions within the largest of the three genera-specific species complexes found on *Aporusa* #51 after the second fogging. Beetle complexes were always composed of morphologically very similar species. S = number of species, Abu. = abundance.

	Chrysomelidae (Eumolpinae)		Curculionidae (Otiorhynchinae)		Anthicidae	
	S	Abu.	S	Abu.	S	Abu.
	1	144	1	49	1	44
	1	38	1	44	1	21
	1	30	1	35	1	13
	1	21	1	14	1	12
	1	15	1	13	1	11
	1	4	3	10	1	10
	1	3	1	8	1	8
	2	2	1	6	1	5
	10	1	1	5	1	4
			1	3	2	3
			1	2	4	1
			1	1		
Σ	19	258	14	190	15	132

DISCUSSION

The initially fogged trees. The Coleoptera of all trees represented around 5% of the individuals of their respective arboreal arthropod community (Floren & Linsenmair 1997). Chrysomelidae, Curculionidae, and Staphylinidae were the only families found regularly in all samples. Since many of the phytophagous groups are considered to consist of many specialists, for example in central Europe 80% of Chrysomelidae are assumed to be mono- or oligophagous (Schöller 1996), we expected to find at least some specialists in these groups. It was, however, not possible to identify specialists among the phytophagous beetles because they were too rare. Pre-sorting of the remaining non-phytophagous beetles did not show any larger overlap of species between trees. Therefore, our data do not allow us to make any statement of tree-specific associations for Coeloptera.

Most typically, Coleoptera communities consisted of rare species showing only little species overlap between trees. This is distinctly different to the ecosystems of the temperate latitudes. For example, in comparable collections in central Europe usually a third of the most common species provides 85% of all individuals. The convention of using a dominance classification, ranking from eudominant to sporadically occurring species (e.g., Engelmann 1978), is therefore not applicable in tropical lowland rain forest.

We never found tree-specific beetle communities, neither between conspecific trees, which were very similar in every respect, nor between repeated foggings of the same tree. This result is confirmed by all the other comparable investigations summarized in Table 6. A classical deterministic structure on the species level, as is usually found in many habitats of the higher latitudes (e.g., Kennedy & Southwood 1984, Hsiao 1985) must therefore definitely be rejected for the system studied by us.

One outstanding general characteristic of the canopy communities was the near total lack of larvae and other little mobile taxa. Although it is known that many species of Coleoptera develop in the soil, for example the common Chrysomelidae subfamilies of Eumolpinae, Alticinae, and Galerucinae (Jolivet 1994), the absence of larvae applied to all groups of

arboreal arthropods. This could be the consequence of the assumed high predatory pressure by ants which, numerically, dominated all trees. They probably prevent most herbivores from depositing their eggs in the crowns (Floren & Linsenmair 1997, 1998). In canopies of temperate ecosystems, in which ants rarely occur in large numbers, larvae of many different taxa (Coleoptera, Symphyta, Lepidoptera etc.) can be found at very high densities.

Our results constitute a further example of the extraordinary diversity of Coleoptera in tropical lowland rain forests. With an overall estimation of 2000 species from only 19 trees, our sample of beetles equals a quarter of all species found in central Europe (Freude *et al.* 1983). In those ecosystems a comparatively small sampling effort would reveal tree-specific arthropod communities (e.g., Nielson 1975, Southwood *et al.* 1982, Basset & Burckhardt 1992, Simandl 1993, Wagner 1996, Floren & Linsenmair, unpubl. results). Thus, Southwood *et al.* (1982) were able to collect almost 40% of the tree-associated phytophagous fauna after fogging two to three individuals of six British tree species. A further example comes from Schmidt (1998) who investigated arthropod communities on young birch trees in Germany. He reached species saturation after sampling only 10 trees. In contrast, all investigations in undisturbed lowland forests of the tropics (see Table 6) show that it is neither possible to estimate the size of the regional species pool nor to give information on the sampling effort necessary to reach species saturation.

The refogging experiments. As our investigations of the fogging efficiency have shown, the arthropod communities of trees of the lower canopy, with their relatively small crowns, can be in large measure quantitatively collected. This was demonstrated by shaking-samples of the trees and by performing control fogs immediately following the two-hour collecting phase as well as by executing thorough observations in the trees before and after the fogging. These results confirm that the small study trees were, after the fogging, to a very large extent 'empty' and soon became very quickly recolonized.

Independent of the time intervals between the first foggings and the refogs, the refog communities showed – with one exception (see below) – the same species abundance patterns as already described for the initially fogged communities. Even on refogged trees we found no convergent development of communities towards their original composition. This shows that it is not the specific characteristics of the tree that determines the structure of a community. Furthermore, this result did not change even after longer time intervals of up to three years between fogs (unpubl. results). The data do not point to the existence of pioneer species, which are specialized at finding and exploiting free resources quickly, from which they are then excluded during further development. Such successions are standard examples in temperate ecosystems (e.g., Bach 1990, Begon *et al.* 1996). They are an indication of deterministic processes which lead to a predictable community species composition.

As the five consecutive daily foggings demonstrate, Coleoptera were able to 'fill' empty tree crowns very quickly. Together with Diptera, beetles provided the fastest colonizers, with abundances that could be similar to those of the first fog (Floren & Linsenmair 1994). During the recolonization we always observed an almost complete species turnover. This is a further indication that arboreal Coleoptera do not establish any form of stable guild equilibrium on the species level.

The only deviations from these results were found after refogging *Aporusa* #51 nine days after the first fog. Here the abundances had increased by almost 350% in relation to the initially fog, without our being able to observe any conspicuous changes in conditions during the time between both fogs. These were the highest abundances and species numbers found in a single tree. Why almost half of all these morphologically similar species were assembled in genera-specific beetle complexes is still not understood. All those species remained rare in the other samples. Their occurrence might be related to a special reproductive strategy and/or a temporary usage of the same resource, but these assumptions are completely speculative. Similar phenomena were repeatedly found in different habitats and biogeographical regions. Baehr, for example, discovered similar species complexes of different families of Coleoptera under the bark of *Eucalyptus* species along river sites (Baehr 1992, pers. comm.) and further collections in Australia added even more groups (Floren unpubl.). Mody found similar species aggregations on shrubs in the savannah of the Comoe National Park in Cote d'Ivoire (Mody, pers. comm.). According to Morawetz, masses of insects from different groups occur sporadically in the crowns of

Venezuelan lowland rain forest trees without showing any correlation with plant phenology or weather conditions (Morawetz, pers. comm.). Thus, it seems justified to cautiously hypothesize that this type of species association may not be purely incidental, but may have some, though as yet unknown, important functional meaning.

Comparison with other studies. The unique composition of the Coleoptera of each tree crown has far-reaching consequences for the interpretation of the data. Since 74% of all species occurred only in a single sample, there is hardly any basis for a more detailed statistical evaluation (compare Ludwig & Reynolds 1988). Moreover, there is almost no knowledge available on the autecology of canopy species. Since most beetle species were found as singletons they should in a strict sense (and according to current methods of evaluation) be regarded as tourists (Moran & Southwood 1982) since one cannot assess whether they belong to the tree-associated fauna or to the non-resident fauna that is dispersing between habitats. In that case, however, nearly all beetles would have been caught purely by chance which we consider unlikely. An additional example that shows how difficult it is to interpret such data, is the discussion about the relationship between specialists and generalists. This question is of special importance when considering the causes of the high diversity of arthropods, and explains the special interest of researchers in trying to determine the proportion of specialists in their investigated communities. Such an estimate is the decisive assumption in Erwin's calculation of global diversity (Erwin 1982), and is also found in the work of Allison *et al.* (1993, 1997) as well as in Mawdsley and Stork's computation of 'effective specialization' (Mawdsley & Stork 1997). Due to the insufficiency of relevant and reliable data, conclusions on the specialist/generalist problem should still be regarded as being very tentative.

Such far-reaching conclusions could only be drawn on the basis of a far more comprehensive sampling which should firstly aim at reaching species saturation of the area investigated. As this does not seem realistic in most cases, autecological studies are the only way to reliably judge the degree of specialization. For herbivores, this is mostly the determination of the proportion of mono- and oligophagous species compared with polyphagous ones. Initial investigations have been made by Basset (1996) and Basset *et al.* (1996), who tested herbivorous arthropods originating from 10 tree species of a mosaic of primary and secondary forest in Papua New Guinea. Their conclusions as to the total number of species within this area, however, are based on many doubtfull assumptions. For example, they assumed a complete sampling of the herbivorous species in the field, transferred the ratio of specialist to generalist species found in the laboratory onto their sample, and referred to questionable data in the literature to estimate the extent of specialization of single taxa. All these assumptions, however, are strongly affected by uncertainties. Basset's conclusion from his data is 'that the ratio of specialists may be very different among tree species and study sites'. Although nobody is at present able to call this into question, it could also be that the high variability is to a much greater extent the consequence of the difficulty of obtaining a complete set of tree-specific herbivores by hand-collecting methods. Our fogging experiments demonstrate that most of the arthropods of lowland rain forest trees are highly mobile and show no species saturation, while less mobile species are almost completely missing (these results are now based on 79 foggings). Therefore, hand-sampling methods will most probably yield only a small fraction of the species pool. This is true in particular for the highly abundant and very diverse groups of Chrysomelidae and Curculionidae, which should contribute many of the generalists and specialists. Furthermore, one has to take into consideration that the species abundance distributions in primary lowland rain forests differ significantly from those within secondary forests. There are hardly any observations of abundant species in primary forests, while in adjacent areas of secondary forests, single arthropod species can usually be found in high abundances. This is clearly shown by our last fogging experiments in secondary forests. Here, many species of different arthropod groups, including caterpillars and some species of Chrysomelidae, Anthicidae, and Malachidae, occurred in distinctly higher abundances compared with primary forests. All these common species disappeared in the course of time and forest regeneration; meanwhile structural complexity and species richness approached those of pristine forests (Floren & Linsenmair, unpubl.). Since Basset used mainly caterpillars and beetles in his feeding experiments, we assume that his study area was not repre-

TABLE 6. Comparable investigations of arboreal Coleoptera communities in tropical lowland rain forests in the literature. (Hammond *et al.* 1997 and Basset *et al.* 1996 used different sampling methods besides canopy fogging). Abbreviations: abun. = abundance; approx. = approximately, fam. = family; herb. = herbivore; ind. = individual; Num. of sp. = number of species; rest. = restricted. The tree species: S. joh. = *Shorea johorensis*; S. mac. = *Shorea macrophylla*; A. lag. = *Aporusa lagenocarpa*; A. sub. = *Aporusa subcaudata*; X. aff. = *Xantophyllum affine*; C. acu. = *Castanopsis acuminatissima*; L. cel. = *Lithocarpus celebicus*. The families of Coleoptera: Chryso. = Chrysomelidae, Staphy. = Staphylinidae, Ptilodacty. = Ptilodactylidae, Mordell. = Mordellidae, Curc. = Curculionidae, Anthi. = Anthicidae, Attelab. = Attelabidae, Bruchi. = Bruchidae, Cocci. = Coccinellidae.

Source	Forest type	Trees sampled by fogging	Most abu. fam.	Absolute numbers	Num. of sp.	% single	% sp. < 10 ind.	Sp. overlap	Sp. saturation
Erwin & Scott 1980, Panama	scrubby seasonal forest	19 Lucha semanni	Chry. Staply. Ptilodacty. Mordell.	7712	954 1200 sp. estimated		at least 60%		
Erwin 1983, Brazil	4 forest types	10 transects of 50m	Curc. Chry. ? ?	24.350	1080			83% restr. To one forest type	
Farrell & Erwin 1988, Peru	5 forest types	three 12x 12m plots in each forest type	Chry. Curc. Staply.			over 500 species with fewer than 5 individuals			
Morse *et al.* 1988, Brunei, Borneo	pr. lowland rain forest	10 trees of 5 species	Chry. Staply. Anthi. Curc.	3919	859	58%	at least 92%		
Mawdsley & Stork 1997, Brunei, Borneo	pr. lowland rain forest	4 S. joh. 2 S. mac. 4 diff. trees		only numbers of sp. per tree				82% restr. to one tree sp.	no
Floren & Linsenmair 1997, Sabah, Borneo	pr. Lowland rain forest, understory	10 A. lag. 5 A. sub. 4 X. aff.	Chry. Staply. Curc.	8856	1183 2000 sp. estimated	59%	96%	smaller 10%	no
Stork & Brendell 1990, Sulawesi	pr. forests, altitudinal gradient	20+m^2 from six 12x 12m plots		9158	1176			little similarity	
Hammond *et al.* 1997, Sulawesi	lowland rain forest	500 ha		18.000	1355	46%			
Allison *et al.* 1993, Papua New Guinea	pr. rain forest altitudinal gradient	6 C. acu. 2 L. cel.	Staply Curc. Chry. Aderidae	4840	633	50.7%	at least 90%	22-31% within, 2-12% between tree sp.	no
Basset *et al.* 1996, Papua New Guinea	mosaic of sec. forest	10 different trees		4696	391				
Allison *et al.* 1997, Papua New Guinea	mid-montane rain forest	8 C. acu.	Chry. Attelab. Staply. Curc.	3977	418	47.6%	85.2%	between 12 and 31%	no
Davis *et al.* 1997, N-Venezuela	4 different trees in dry deciduous and 2 in riparian forests		Bruch. Curc. Anobidae Cocci.	6132	978				no

TABLE 6. Continued.

Source	Forest type	Trees sampled by fogging	Most abu. fam.	Absolute numbers	Num. of sp.	% single	% sp. < 10 ind.	Sp. overlap	Sp. Saturation
Wagner 1996, 1997, East Rwanda	dry forest	4 *Lannea fulva*	Anthri. Anobiinae	886	84	67.5%			no
Wagner 1996, 1997, East Rwanda	gallery forest	8 *Teclea nobilis*	Chry. Apionidae Curc.	4594	230	56.2%			yes
Wagner 1996, 1997, West Rwanda	montane rain forest	9 *Capra grandiflora*	Chry. Staply. Curc. Cocci.	2820	397	55%			no
Wagner 1996, 1997, Congo	upper lowland rain forest	5 *Capra grandiflora*	Chry. Staply. Curc.	242	137	86%		little similarity	no

sentative of a primary lowland evergreen tropical forest. Therefore, Basset's results should be seen as an initial experiment-based assessment of the generalist/specialist problem in more or less disturbed guilds of tropical herbivorous insects, but they seem not be suitable as an explanation of the situation in mature lowland rain forests.

Altogether, one can conclude that the arboreal Coleoptera of primary lowland rain forests resemble non-interactive communities in the sense of Cornell and Lawton (1992), which have to be regarded as non-equilibrium communities (Wiens 1984). In order to gain more knowledge of the structuring mechanisms of these communities more basic work has to be conducted. In particular, this demands further investigations into the distribution patterns and autecology of representative samples of species forming the most important guilds.

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