

ICHNEUMONIDAE (HYMENOPTERA) FROM THE CANOPY OF TROPICAL FORESTS IN SABAH, MALAYSIA: A COMPARISON BETWEEN PRIMARY AND SECONDARY FORESTS

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Abstract. We collected arthropods from the canopies of secondary forests with differing disturbance levels at seven sites near Kinabalu National Park (Sabah, northern Borneo, Malaysia) by selective canopy fogging, and compared the results with those earlier obtained from primary rain forest in the National Park. The samples contained few individuals but many species of Ichneumonidae (Insecta, Hymenoptera). The abundance of Ichneumonidae was rather similar among the forest sites, although the abundance of Araneida and Formicidae (potential predators) was much lower in the secondary than in the primary forest, and although the abundance of Lepidoptera larvae (the most important host group) differed between different forest sites. The species numbers in the secondary forests were lower than those in the primary forest by a factor of about 2. The subfamily composition of Ichneumonidae was not noticeably affected by the age of the forests, but it was different in samples from different tree species. Some indicators of α -diversity (relative number of species, percentage of singletons, evenness) were distinctly higher in our samples from the canopy of primary and secondary forests than in other samples from temperate and tropical habitats analyzed so far. Because of the very high numbers of rare species, the sample size is much too small to reach species saturation. In addition, species estimators produce unreliable results, and we are unable to calculate real species numbers. *Accepted 12 November 2004.*

Key words: Borneo, canopy, diversity, Hymenoptera, Ichneumonidae, primary forests, recolonization, secondary forests, species richness.

INTRODUCTION

For several years wasps of the family Ichneumonidae (Hymenoptera) were considered to be one of the few larger taxa of arthropods which are not more diverse and species-rich in the tropics than in temperate regions (Owen & Owen 1974, Janzen & Pond 1975, Gauld 1986, Noyes 1989, Stork 1991). In a previous paper on samples collected by canopy fogging in a primary lowland rain forest in Sabah (northern Borneo, Malaysia) (Horstmann *et al.* 1999), we demonstrated that species richness and α -diversity of Ichneumonidae in this habitat are much higher than in other samples from both temperate and tropical habitats analyzed so far. But we had to compare the results with those obtained in the canopy of a German managed forest, because undisturbed primary forests large enough to avoid island effects are virtually absent in central Europe (Peterken 1996). On the other hand, secondary forests in all stages of anthropogenic dis-

turbance and regeneration are widespread in the tropics. A study of the ichneumonid communities of these forests allows comparison with results from primary forests in the tropics as well as secondary forests in temperate regions.

MATERIAL AND METHODS

Field work was carried out in Sabah (northern Borneo), Malaysia. Seven sites in three areas were chosen for canopy fogging: three forest types of differing disturbance levels at Sorinsim on the border of the Kinabalu National Park (= Kinabalu NP), three forest types of differing disturbance levels near the Crocker Range National Park (= Crocker Range NP), and two isolated trees in the village of Kibbas (all sites at 300–700 m a.s.l.) (Fig. 1). The results are compared with those previously obtained in a primary forest near Poring Hot Spring (abbreviated P), a mature lowland rain forest in Kinabalu NP (at 500–700 m a.s.l.) (Floren & Linsenmair 1997, Horstmann *et al.* 1999).

The three sites near Sorinsim (abbreviated SI, SII, and SIII respectively) have already been described in

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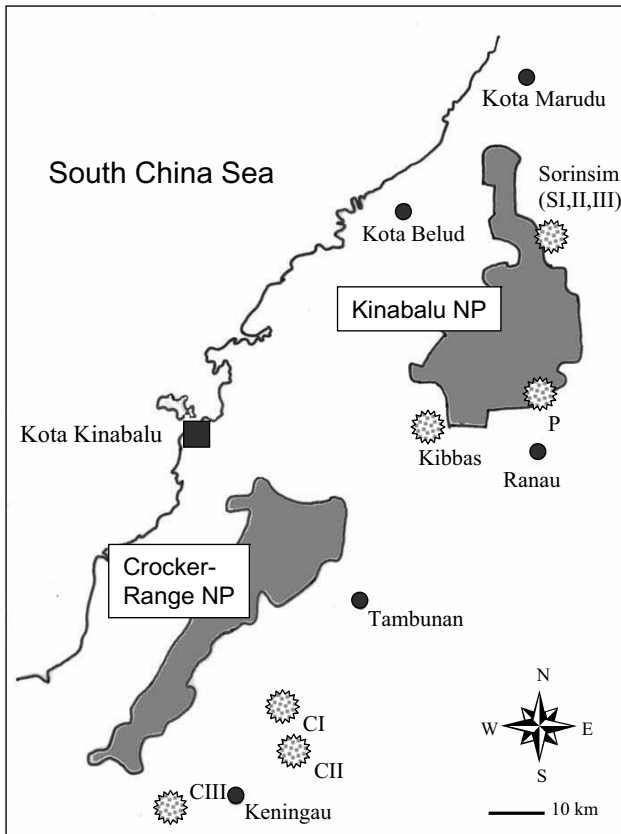


FIG. 1. Map of research sites in the Kinabalu region of Sabah, northern Borneo. Dots refer to areas where foggings were carried out (for more details see text). P = Poring Hot Spring.

detail (Floren & Linsenmair 1999, 2001, 2003). The forest was clear-cut for agricultural use and then left to regenerate for 5, 15, and approximately 40 years respectively. The forests were adjacent to one another, and SIII merged into primary hill forest (Floren & Linsenmair 2001). All of these forests had only a single canopy layer which was in no case closed. In SI almost only pioneer trees grew, and ten individuals of the common species *Melochia umbellata* (Sterculiaceae) were selected (height of the fogged trees 6–8 m, crown projection 20–34 m²). In addition, samples were taken from two trees of *Vitex pinnata* (Verbenaceae), the focal tree species of SII, which was rare in SI. The trees produced little shade and the undergrowth was formed by dense grass and low bushes. All in all, the number of tree species even in this 5-year-old forest was estimated to be around 50 (Biun, pers. comm.). In SII eleven individuals of the

most common tree species *Vitex pinnata* were chosen (height about 20 m, crown projection 21–54 m²). On the ground, the grass and shrub cover was replaced by a dense growth of tree saplings. In SIII, where ten individuals of *Vitex pinnata* were selected (height about 20 m, crown projection 25–67 m²), this species was markedly rarer and the trees were visibly older than in SII (with dead and partly rotten branches, etc.). On the ground, the growth of tree saplings was thinner and distinctly more dead wood was found than in the younger forest types. Very evidently, tree diversity increased with the age of the regenerating forest. All trees were fogged for the first time in the period 16 February–8 March 1997. Three trees (one in each of SI, SII and SIII) were fogged four or five times on consecutive days, another three trees (one in each of SI, SII and SIII) were re-fogged after an interval of 9–10 days, and one additional tree (in SI)

was fogged five times on consecutive days (one attempt failed because of bad weather conditions) and then again twice after an interval of 12 days (Table 4).

The three sites near Crocker Range NP (abbreviated CI, CII, and CIII respectively) were man-made, isolated forest islands (size: 4–6 ha) in an area of cultivated land (plantations of bananas, oil palms, rubber plants or rice, pastures), the shortest distance to a primary forest (Crocker Range NP) being about 10 km (Fig. 1). The sites had been cleared (mostly burned), used for agriculture for some years, and then left to regenerate. These forests, too, had only a single, never closed canopy layer. In all sites, *Melanolepis* sp. (Euphorbiaceae) belonged to the commonest tree species and therefore individuals of this species were mostly used for canopy fogging. The forest in CI was approximately 10 years old and consisted mainly of pioneer trees, with a dense undergrowth of bushes and climbing plant species. No older trees were present, and there were no older forests at a distance of less than 5 km. Eight individuals of *Melanolepis* sp. and one individual of *Clerodendron* sp. (Verbenaceae) were chosen for fogging (height 6–8 m, crown projection 16–26 m²). The forest in CII, situated 5 km from CI, was approximately 20 years old. Almost all trees of the single canopy layer belonged to *Melanolepis* sp., seven of which were fogged (height about 18 m, crown projection 20–35 m²). The undergrowth was similar to that in CI. In CIII, situated about 30 km from CI and CII, the forest was approximately 50 years old. Eight individuals of *Melanolepis* sp. and one individual of *Saraca dentata* (Pabaceae) were selected (height 18–25 m, crown projection 20–40 m²). On the ground, a dense growth of tree saplings and young trees was found, but almost no climbing plant species and only a few dead and rotten trees. All trees were fogged in the period 19–21 February 2001.

Two isolated trees on the edge of the village of Kibbas (abbreviated K) were fogged on 19 March 1998: one individual of *Vitex pinnata* (height 8 m, crown projection 40 m²) and one individual of *Cinnamomum griffithii* (Lauraceae) (height 6 m, crown projection 42 m²). The latter was inhabited by a large colony of *Oecophylla smaragdina* (Formicidae). Many other more or less isolated trees were present around the village, the shortest distance from that area to a primary forest (Kinabalu NP) being about 5 km.

The method of selective canopy fogging is described in detail by Floren & Linsenmair (1997). Because of the simpler forest structure in the secondary forests, with only one canopy layer, no roof had to

be constructed above the trees in order to separate them from an upper canopy layer (Floren & Linsenmair 1999). The vegetation beneath the study tree was cut and 80–90% of the crown projection was covered with funnels. All trees in secondary forests were fogged in daytime, early in the morning when there was little wind drift. Fogging was conducted from the ground or from within the tree crown, depending on the size of the tree and the weather conditions. We used natural pyrethrum (in 2% concentration, dissolved in a highly refined white oil) as insecticide, which biodegrades under the influence of light in a few hours into non-toxic components.

Since the mean body size of Ichneumonidae possibly varies according to habitat (Townes 1958, Horstmann 1992), the thorax length was ascertained, the distance between the anterior edge of the mesoscutum and the posterior edge of the propodeum being measured (Horstmann *et al.* 1999).

Community structure was analyzed by calculating α -diversity indices and species accumulation curves (Shinozaki curves). Instead of Shannon-Wiener's index of diversity (Hs), which depends on the numbers of species (S) in the samples, we used the evenness index (Hs/ln S) (for formulae see Fisher *et al.* 1943 and Floren & Linsenmair 1997). Species numbers were estimated by several species estimators, namely Chao 2, Chao & Lee, jackknife, bootstrap, Michaelis-Menten (for detailed descriptions see Colwell 2000).

RESULTS

Abundance of some major taxa of Arthropoda and Hymenoptera. The influence of anthropogenic disturbances on the structure of arboreal arthropod communities has already been studied in the area by Floren & Linsenmair (1999, 2001, 2003), these studies being based on material from primary forests near Poring Hot Spring and from secondary forests near Sorinsim. Here we present data on some arthropod taxa which may act as predators or as hosts of Ichneumonidae (Table 1). In secondary forests the abundance of ants was much lower than in primary forest (Mann-Whitney U-test, $P < 0.001$), it was lower in the Crocker Range than in the Sorinsim forests ($P < 0.001$), and at both forest sites it was lowest in the youngest forests ($P < 0.05$). An exception was the sample from Kibbas, caused by the extremely high abundance of *Oecophylla smaragdina* on one of the two trees. Araneida were also less abundant in the secondary forests ($P < 0.03$). In the Sorinsim forests,

TABLE 1. Mean numbers of individuals of some major Arthropoda taxa and subgroups of Hymenoptera in canopy fogging samples from secondary forests near Sorinsim, Crocker Range NP, and Kibbas (primary day fogs) and a primary rain forest in Kinabalu NP (primary day fogs and primary night fogs), all in Sabah, northern Borneo, calculated for one fog and for a crown projection of 1m² and a leaf cover of 100 % (n: number of fogs). For Ichneumonidae the mean thorax length is also indicated.

Taxa	Sorinsim			Crocker Range			Kibbas	Kinabalu NP	
	SI (n=12)	SII (n=11)	SIII (n=10)	CI (n=9)	CII (n=7)	CIII (n=9)	K (n=2)	Day (n=25)	Night (n=14)
All Arthropoda	173.8	169.1	283.6	179.1	193.8	191.8	629.8	350.8	369.4
Araneida	11.9	7.9	14.7	18.6	12.2	11.6	14.6	19.7	21.7
Coleoptera	29.7	13.1	33.3	26.9	21.8	15.6	42.6	17.6	20.3
Diptera	15.5	13.3	33.4	44.0	36.6	27.5	6.5	21.7	33.4
Lepidoptera, larvae	11.8	6.3	10.3	3.3	1.3	4.3	2.0	3.8	2.8
Lepidoptera, adults	0.4	0.3	0.3	1.9	2.6	1.2	1.1	0.6	1.4
Formicidae	56.3	82.9	107.5	12.5	52.6	41.3	396.9	180.1	192.6
Hymenoptera except Formicidae	6.3	4.7	11.6	18.6	9.1	15.5	15.2	8.6	13.7
Microhymenoptera	4.84	3.21	9.15	13.53	6.13	9.68	11.18	5.66	9.70
Braconidae	0.80	0.89	1.70	4.05	2.54	4.49	2.05	2.15	2.98
Ichneumonidae	0.15	0.36	0.38	0.42	0.28	0.23	0.55	0.36	0.49
Thorax length (mm)	1.59 (for all specimens from secondary forests)							1.38	2.00
Aculeata	0.47	0.22	0.35	0.52	0.18	1.07	1.43	0.43	0.55

the abundance of Lepidoptera larvae was higher than in the Crocker Range forests ($P < 0.001$). On the other hand, the abundance of Diptera and of non-formicid Hymenoptera was somewhat higher in the Crocker Range forests ($P < 0.004$). The abundance of Coleoptera was rather similar among the forest sites. The resulting abundance of Arthropoda was markedly lower in the secondary forests ($P < 0.001$), again with the exception of the Kibbas sample.

About 70 % of the non-formicid Hymenoptera were Microhymenoptera (and 60–70 % of these were Chalcidoidea). Braconidae were more abundant than Ichneumonidae by a factor of 7, and the former were much more abundant in the Crocker Range than in the Sorinsim forests ($P < 0.001$). Symphyta were very rare (only four adults found in all samples from secondary forests). Altogether 13 101 specimens of non-formicid Hymenoptera were collected by canopy fogging in secondary forests, 365 of which were Ichneumonidae.

Abundance and species composition of Ichneumonidae. The Ichneumonidae were determined to genera and assigned to 180 morphospecies (Appendix 1). The

abundance of Ichneumonidae in the secondary forests was rather similar among the forest sites, except for SI where the abundance on trees of the species *Melochia umbellata* was much lower (Mann-Whitney U-test, $P < 0.005$) (Table 1). The subfamily composition of Ichneumonidae also did not vary much between most of the samples, in particular it was not noticeably affected by the age of the trees (Table 2). Cryptinae and Orthocentrinae were the most frequent subfamilies, and Pimplinae, Campopleginae and Mesochorinae were also rather common at all sites. But there were differences between samples fogged from different tree species. The low abundance of Ichneumonidae in samples from *Melochia umbellata* was mainly caused by the low abundance of Cryptinae (no Cryptini, only a few Phygadeuontini). In samples from *Melochia umbellata* (SI) Cryptinae were therefore less frequent than Orthocentrinae, whereas in samples from *Vitex pinnata* (SII and SIII) they were more frequent (2 x 3 table Chi²-test, $P < 0.001$). The two samples from *Vitex pinnata* in SI contained seven specimens of Cryptinae, three of Campopleginae and one of Orthocentrinae. This species composition was similar to that of samples from the same tree species in SII

TABLE 2. Subfamily composition of Ichneumonidae (% of individuals) in canopy fogging samples from secondary forests near Sorinsim, Crocker Range NP, and Kibbas (all available day fogs) and a primary rain forest in Kinabalu NP (primary day fogs), all in Sabah, northern Borneo (n: number of individuals, I: idiobionts, K: koinobionts). For SI only samples from *Melochia umbellata* and for CI and CIII only samples from *Melanolepis* sp. were included in the calculation. The percentage of idiobiont individuals in the samples is also given.

Subfamilies	Sorinsim			Crocker Range			Kibbas	Kinabalu
	SI (n=45)	SII (n=88)	SIII (n=91)	CI (n=29)	CII (n=31)	CIII (n=28)	K (n=31)	P (n=127)
Pimplinae (I, K)	8.9	10.2	9.9	0	3.2	7.1	6.4	12.6
Cryptinae (I)	15.6	54.5	48.4	17.2	16.1	17.9	19.4	29.9
Ichneumoninae (I)	6.7	3.4	0	0	0	0	0	0.8
Banchinae (K)	4.4	0	1.1	3.4	0	0	3.2	0
Campopleginae (K)	6.7	9.1	11.0	13.8	12.9	7.1	6.4	6.3
Cre mastinae (K)	4.4	1.1	2.2	3.4	0	7.1	6.4	2.4
Tersilochinae (K)	4.4	0	0	6.9	6.4	7.1	6.4	3.9
Mesochorinae (K)	17.8	2.2	5.5	3.4	6.4	3.6	48.4	7.1
Orthocentrinae (K)	26.7	15.9	15.4	37.9	41.9	28.6	3.2	27.6
Metopiinae (K)	2.2	1.1	4.4	3.4	9.7	10.7	0	5.5
Others (I, K)	2.2	2.2	2.2	10.3	3.2	10.7	0	3.9
Idiobionts	29	65	60	28	16	25	23	42

and SIII but quite different from samples collected from *Melochia umbellata* at the same time in the same forest ($P < 0.001$). Because the great majority of species were rare and were present in the samples only as singletons (Table 3), the ichneumonid community

could not be analyzed at a species level. The Kibbas sample was exceptional: five species of Mesochorinae, two of them in rather high numbers, were fogged from one tree (*Vitex pinnata*). On the other hand, only one specimen of Orthocentrinae was collected. The

TABLE 3. Numbers of species (S) and individuals (N), values for α -diversity [percentage of singletons (% of S), Berger-Parker's index (% of N), Williams' alpha and evenness (Hs/ln S)], and estimated species numbers calculated with species estimators (ESN, mean and standard deviation), calculated for all available canopy fogging samples from secondary forests near Sorinsim, Crocker Range NP, and Kibbas (day fogs) and a primary rain forest in Kinabalu NP (day fogs and night fogs), all in Sabah, northern Borneo.

Indices	Sorinsim				Crocker Range				Kibbas	Kinabalu NP		
	SI	SII	SIII	S all	CI	CII	CIII	C all	K	Day	Night	P all
Species	41	56	53	121	28	23	29	68	18	159	79	220
Individuals	56	88	91	235	36	31	32	99	31	221	98	319
Singletons	80	71	74	69	79	78	90	72	67	84	81	77
B.-P. index	10.7	14.8	6.6	9.8	11.1	12.9	6.2	5.0	19.6	5.9	3.1	4.4
W. alpha	69	66	53	100	58	40	150	96	18	254	190	313
Evenness	0.96	0.92	0.94	0.91	0.97	0.96	0.99	0.97	0.92	0.94	0.98	0.96
ESN, mean				212				171	30	371	163	476
s. d.				60				100	7	153	67	166

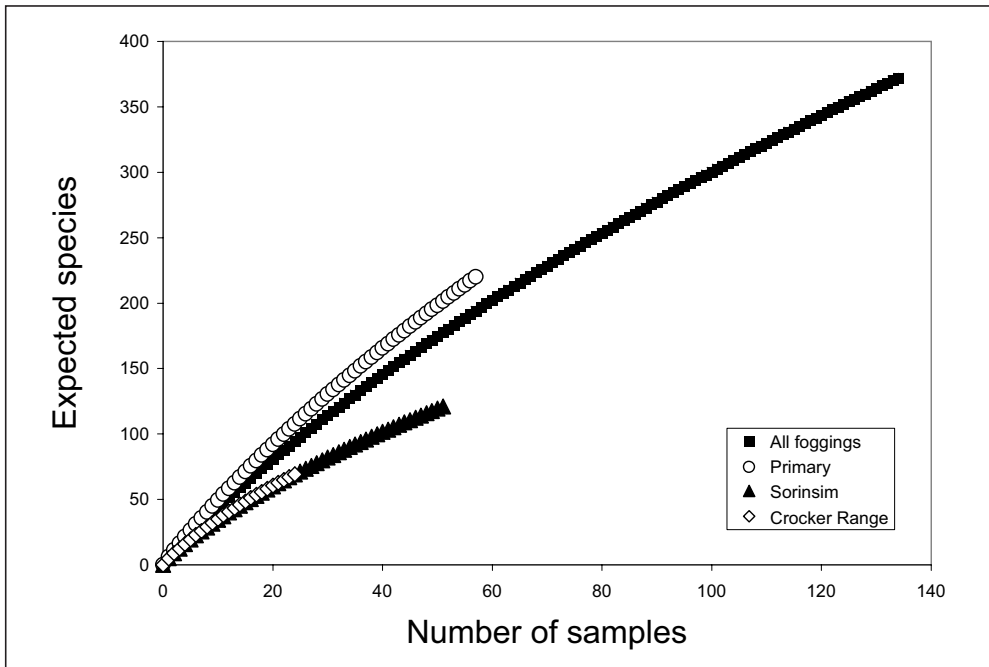


FIG. 2. Species accumulation curves (Shinozaki curves) of the Ichneumonidae communities, calculated for a primary rain forest in Kinabalu NP; for two secondary forest sites near Sorinsim and Crocker Range NP; and for all fogging samples collected in the Kinabalu region of Sabah, northern Borneo.

latter result is not singular: at the same time (March 1998), 11 trees were fogged at night in the primary forest (see Appendix 2), and in these samples the Orthocentrinae were also rare, contrary to all other samples from day fogs and night fogs obtained in the period 1992–1996 (Horstmann *et al.* 1999). The percentages of idiobiont individuals (idiobionts kill their host at or shortly after oviposition, whereas koinobionts allow their hosts to grow after oviposition; Haeselbarth 1979, Askew & Shaw 1986) varied much between the forests (Table 2). The mean thorax length of Ichneumonidae was higher in secondary forests than in day fog samples from primary forest by a factor of 1.2 (Mann-Whitney U-test, $P < 0.005$) (Table 1).

As is demonstrated by the Shinozaki curves (Fig. 2), the species richness in the secondary forests should be almost identical between the Sorinsim and Crocker Range forests, but lower than in the primary forest. In no forest type was the sampling effort for Ichneumonidae sufficient to collect even a moderate proportion of the species present in that habitat, and the same went for the total region. Mean species num-

bers (with standard deviations) calculated by species estimators are noted in Table 3. For the canopies of all forests studied in the Kinabalu region, the species estimators calculate 668 ± 184 species.

Values for α -diversity were high (Table 3). The relative species number (species number divided by sample size), the percentage of singletons, and the evenness do not differ between samples from secondary and from primary forests. Williams' alpha was higher in samples from primary forest than from secondary forests, and also from other temperate and tropical habitats analyzed so far (listed by Horstmann *et al.* 1999) (Mann-Whitney U-test, $P < 0.02$). Berger-Parker's index was also low in samples from primary forest (thus indicating a high α -diversity), but this parameter proved to be very variable even in samples from the same habitat (Horstmann 1992). In the Sorinsim series, α -diversity was highest in the youngest forest, while in the Crocker Range series it was highest in the oldest forest (being about as high as in the primary forest), but the differences were small and not significant. Samples from the primary forest (alto-

gether 66 samples, 220 species) and the Sorinsim forests (53 samples, 121 species) had 22 species, samples from the primary forest and the Crocker Range forests (25 samples, 68 species) had 15 species, and samples from the Sorinsim forests and the Crocker Range forests had 18 species in common. Sørensen's index for the three pairs of areas amounted to 0.13, 0.10, and 0.19 respectively.

Re-fogging experiments. In the primary rain forest, one tree was fogged five times on consecutive days, and another was re-fogged after an interval of nine days (Floren & Linsenmair 1998). But the numbers of Ichneumonidae in these samples were too small to allow an analysis of short-term recolonization. With the inclusion of the samples from the Sorinsim secondary forests, four series collected under each of the two sampling regimes are available. The numbers of Ichneumonidae are still rather small, and the variability is high. Therefore the values from the four series of each sampling regime are summed. In trees which were re-fogged daily, the abundance of non-formicid Hymenoptera in the second sample went down to 25 %, that of Microhymenoptera to 22 %, and that of Ichneumonidae to 32 % of the first sample, and remained rather constant on subsequent days (mean values 24 %, 22 % and 39 % respectively of the first sample). In trees which were re-fogged after 9–10 days, the abundance of non-formicid Hymenoptera in the second sample climbed to 56 %, that of Microhymenoptera to 49 %, and that of Ichneumonidae to 66 % of the first sample.

One tree in SI was fogged seven times during a period of 19 days (Table 4), and the results from this series are irregular and are therefore presented separately. The composition of the first sample was unremarkable (about the same as noted for all SI fogs in Table 1), but in subsequent samples the abundance of non-formicid Hymenoptera went up, until it reached a maximum in the sixth and seventh sample. This was mainly caused by an increase in numbers of one species, the fig wasp *Kradibia* sp. (Agonidae, Chalcidoidea) (Vidal det.). But more than one species was certainly involved, because the abundance of Chalcidoidea (without *Kradibia* sp.) and Proctotrupoidea also went up, while the abundance of other taxa did not go down.

DISCUSSION

As in samples from primary rain forest in the Kinabalu NP, few individuals but many species of Ichneumonidae were collected in the canopy of neighboring secondary forests, whereas Microhymenoptera and Braconidae were much more abundant in all samples. The abundance of Ichneumonidae (calculated as numbers of individuals from standardized parts of trees) in the canopy of secondary forests (except for SI; see below) was as low as the values obtained in primary forest. Neither did the subfamily composition of Ichneumonidae differ much between primary and secondary forests. The percentages of idiobiont individuals in the samples from secondary forests were not substantially different from those in samples from

TABLE 4. Numbers of individuals of Formicidae, of non-formicid Hymenoptera, and of several subgroups in seven samples, collected by canopy fogging from one tree specimen of *Melochia umbellata* during a period of 19 days in a secondary forest (site SI) near Sorinsim in Sabah, northern Borneo.

Taxa	21.02.97	22.02.97	24.02.97	25.02.97	26.02.97	10.03.97	11.03.97
Formicidae	146	50	26	22	7	75	52
Hymenoptera (except Formicidae)	119	134	349	400	175	913	858
Chalcidoidea (except <i>Kradibia</i> sp.)	41	20	83	88	18	151	107
<i>Kradibia</i> sp.	7	3	31	46	16	517	641
Proctotrupoidea	32	40	125	185	104	174	69
Ceraphronoidea	2	27	28	40	16	10	10
Cynipoidea	13	21	55	20	11	17	10
Braconidae	16	8	8	10	6	28	12
Ichneumonidae	1	2	4	5	2	2	5
Aculeata	7	13	15	6	2	13	4

primary forest or from habitats in Europe. That the Ichneumonidae from secondary forests were on average larger than those from primary forest corresponds with the hypothesis that the danger of desiccation for small specimens might be lower in the lower canopy layer of a primary rain forest than in the open canopy of a young secondary forest. An alternative explanation might be that species with larger individuals reach the young forests quicker. Some values for α -diversity in the secondary forests (relative number of species, percentage of singletons, evenness) were as high as in the primary forest and distinctly higher than in samples from other temperate and tropical habitats analyzed so far (listed by Horstmann *et al.* 1999) (Mann-Whitney U-test, $P < 0.001$). The data from re-fogging experiments support earlier results, namely that the recolonization of the fogged trees by parasitoids or by their hosts requires time (probably months) and that Ichneumonidae are better colonizers than Microhymenoptera. These phenomena were already discussed in our earlier paper on Ichneumonidae from a primary rain forest (Horstmann *et al.* 1999).

The abundance of potential predators (Araneida and Formicidae) was much lower in the canopy of secondary than of primary forests (by a factor of 2–6, if both groups of predators are combined), and the abundance of Lepidoptera larvae was about three times as high in the Sorinsim as in the Crocker Range forests and the primary forest. But the abundance of Ichneumonidae (and of all parasitic Hymenoptera) was not noticeably affected by these different conditions, although Rathcke & Price (1976) assert that predation pressure should structure parasitoid communities, and although Lepidoptera are an important host group of ichneumonids (Horstmann *et al.* 1999 and literature cited in that paper). It was already hypothesized that predation on adult ichneumonids by ants and spiders might be insignificant (Horstmann *et al.* 1999). We cannot explain these phenomena, because our knowledge of host-parasitoid relationships in Ichneumonidae from southeast Asia is restricted to a few species (Gupta 1987, Yu 1999) and data on the ecology of ichneumonids living in the canopy of tropical forests are lacking. Finally, no influence of the distance between a secondary forest and the nearest primary forest on the abundance and species richness of Ichneumonidae in the secondary forests could be found, while the abundance of Braconidae was even higher in the Crocker Range samples collected far from primary forests (Table 1).

Explanations are possible for two deviant results. First, in samples from *Melochia umbellata* in SI the abundance of Cryptinae was much lower than in other samples collected in the Sorinsim forests. These trees were very young pioneer trees with a thin and smooth bark. Many species of Cryptinae, however, belong to the guild of bark-inhabiting ichneumonids with specialized ovipositors and a mimetic wing pattern (Gauld 1987, Horstmann & Floren 2001), for which hosts may have been lacking here. Second, in all samples collected in March 1998 species of Orthocentrinae were rare. The biology of Orthocentrinae in the tropics is poorly known; they live in shaded and humid habitats and the few known hosts are larvae of Mycetophilidae and Sciaridae (Diptera) (Gauld 1995). The rareness of Orthocentrinae in spring 1998 may have been the consequence of a heavy drought during the preceding half-year, caused by the 1997–1998 El Niño/Southern Oscillation in Malaysia and Indonesia. Perhaps the habitats of hosts and parasitoids on the trees (fungi, rotten wood, cavities with organic detritus) (Floren *in press*) had become dried out.

The irregular results found in the re-fogging series from one tree specimen in SI have already been discussed by Floren & Linsenmair (1999) at the level of non-formicid Hymenoptera. Fig wasps of the genus *Kradibia* pollinate *Ficus* trees (Moraceae) (Wiebes 1978), and possibly the female wasps were hatching from or were attracted by a *Ficus* tree growing near by. But we cannot explain the rise in numbers of other groups of parasitoids in the same series. These results are the more remarkable because the two other re-fogging series collected during the same period from other specimens of the same tree species in SI are quite similar to series from other sites. Floren & Linsenmair (1998) obtained similar results for Coleoptera in one re-fogging series from primary rain forest in Kinabalu NP and discussed the phenomenon, but could arrive at no explanation.

In spite of the fact that fogging samples from 146 trees (17 tree species) in primary and secondary forests are now available from the Kinabalu region, we collected only 684 individuals and 373 morphospecies of Ichneumonidae, and we are unable to calculate real species numbers because the sample size is still much too small. This is demonstrated by the slopes of the species accumulation curves (Shinozaki curves) for Ichneumonidae, which are far from reaching zero. Nor do the low values of Sørensen's index indicate a high β -diversity, for which we lack the basis even to make an educated guess, but rather demonstrate how

far we are from reaching species saturation (Wolda 1981). Thus the situation is similar to that of the beetle community in the same region (Floren & Linsenmair 1998, 2003) and quite different from that of the ant community, where, with the same sampling effort, the sample size was large enough to represent the local species pool of arboreal ants (Floren & Linsenmair in press). Different species estimators produce very different results for one and the same sample, the difference between the highest and the lowest value being about as high as the mean, and the mean species number produced by species estimators depends heavily on sample size. The day fog and night fog samples from the primary forest were most probably taken from the same ichneumonid community (Horstmann *et al.* 1999; see Appendix 2), therefore the species numbers calculated from both samples and from the united sample should be similar. But the species estimators produce quite different results (Table 3), probably caused by the extreme species composition of the ichneumonid community: almost no dominant species, the great majority of species being present as singletons (Soberon & Llorente 1993, Peterson & Slade 1998). Again the situation is different from that of the ant community, for which species estimators calculate reliable species numbers (Floren & Linsenmair in press). Obviously the species numbers of Ichneumonidae in the canopy of the primary forest are higher than those in the canopy of secondary forests (Fig. 2), possibly by a factor of 2 (a rough estimate). But this difference might partly be counterbalanced by an opposite difference in the (unknown) ichneumonid community of the undergrowth, the latter being more richly developed in the secondary than in the primary forests. The rather high value of Sørensen's index calculated for the Sorinsim and the Crocker Range samples may indicate that the ichneumonid communities of the two secondary forests are more similar to each other than each of them is to that of the primary forest. Clearly, however, the species numbers and the values for α -diversity in the canopy of all forests studied in the Kinabalu region are much higher than those in the canopy of a German managed forest (Horstmann *et al.* 1999), the only other forest from which sufficient data on samples collected by canopy fogging are available. Obviously the canopies of primary and secondary tropical forests, at least in southeast Asia, are inhabited by a very large but unknown number of rare or rarely collected species of Ichneumonidae (Horstmann *et al.* 1999, Gauld 2002).

ACKNOWLEDGMENTS

We thank the director of Sabah Parks, Datuk Ali Lamri, for permission to work in the Kinabalu Park, and Alim Buin and Jameli Nais for various kinds of support. For participation in the field work we are much indebted to André Kessler and Stefan Otto. Stefan Vidal (Institut für Pflanzenpathologie und Pflanzenschutz, Göttingen) kindly determined the fig wasp, *Kradibia* sp. (Agaonidae). Mark R. Shaw (National Museums of Scotland, Edinburgh) gave useful comments and assisted us with the English. Financial support for this study came from the German Science Foundation (DFG), Li 150/13-4.

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APPENDIX 1. Ichneumonidae from secondary forests in Sabah, Malaysia

The Ichneumonidae from all canopy fogging samples from secondary forests near the Kinabalu NP in Sabah are listed here, sorted to subfamilies, tribes, genera and species, with the numbers of specimens per species given in brackets.

Pimplinae Ephialtini:	<i>Acrodactyla</i> sp. a (1), <i>Clistopyga</i> sp. a (1), <i>Sinarachna</i> sp. a (1), <i>Zaglyptus</i> sp. a (2), ? <i>Zaglyptus</i> sp. b (1), <i>Zatypota</i> sp. a–e (3; 1; 2; 1; 1); Pimplini: <i>Theronia</i> sp. a (2), <i>Xanthopimpla</i> sp. a–f (1; 1; 2; 6; 1; 1).
Rhyssinae:	<i>Epirhyssa</i> sp. a (1), <i>Lytarmes</i> sp. a (1).
Xoridinae:	<i>Xorides</i> sp. a–b (1; 1).
Tryphoninae: Oedemopsini:	<i>Neliopisthus</i> sp. a (1).
Brachycyrtinae:	<i>Brachycyrtus</i> sp. a (4).
Cryptinae: Phygadeuontini:	<i>Astomaspis</i> sp. a (1), ? <i>Astomaspis</i> sp. b (1), <i>Bentyra</i> sp. a–c (1; 1; 1), <i>Dichrogaster</i> sp. a (1), <i>Gnotus</i> sp. a (1), <i>Handaoia</i> sp. a (1), <i>Lienella</i> sp. a (1), <i>Neopimpla</i> sp. a (1), <i>Orientohemiteles</i> sp. a–b (1; 1), ? <i>Orthizema</i> sp. a (3), <i>Palpostilpnus</i> sp. a–d (2; 1; 1; 1), <i>Paraphylax</i> sp. a–r (14; 2; 1; 5; 2; 1; 1; 1; 1; 2; 2; 1; 1; 2; 1; 1; 2; 1; 1; 2), ? <i>Paraphylax</i> sp. s–t (1; 1), <i>Stibeutes</i> sp. a (2), ? <i>Xenoblytus</i> sp. a (2), Gen. sp. a (1); Cryptini: <i>Ateleute</i> sp. a (1), <i>Dagathia</i> sp. a (1), <i>Eurycryptus</i> sp. a (1), <i>Goryphus</i> sp. a–i (23; 2; 1; 9; 1; 1; 1; 2; 1), ? <i>Goryphus</i> sp. j (2), ? <i>Gotra</i> sp. a (6), <i>Isotima</i> sp. a (1), <i>Listrognathus</i> sp. a (1), <i>Mesostenus</i> sp. a (3), <i>Torbda</i> sp. a (1), <i>Xoridescopus</i> sp. a–b (1; 1).
Ichneumoninae: Alomyini:	<i>Tycherus</i> sp. a (1); Ichneumonini: <i>Barichneumonites</i> sp. a (1), <i>Cushmaniella</i> sp. a (1); Joppocryptini: ? <i>Allonotus</i> sp. a (1); Listrodromini: ? <i>Validentia</i> sp. a (1); Oedicephalini: <i>Satrius</i> sp. a (1).
Lycorininae:	<i>Lycorina</i> sp. a (1).
Banchinae: Atrophini:	<i>Leptobatopsis</i> sp. a–d (2; 1; 1; 1).
Campopleginae:	? <i>Campoplex</i> sp. a (1), <i>Casinaria</i> sp. a (1), <i>Charops</i> sp. a (4), <i>Chriodes</i> sp. a (2), <i>Echthronomas</i> sp. a (1), <i>Eriborus</i> sp. a–g (11; 2; 2; 1; 1; 1; 2), ? <i>Hyposoter</i> sp. a–b (1; 1), <i>Phaedroctonus</i> sp. a (2), ? <i>Phobocampe</i> sp. a (1), <i>Scenocharops</i> sp. a (1), <i>Venturia</i> sp. a–b (1; 1), <i>Xanthocampoplex</i> sp. a (1).
Ophioninae:	<i>Enicospilus</i> sp. a (1).
Cremastinae:	<i>Pristomerus</i> sp. a–d (2; 1; 2; 1), <i>Trathala</i> sp. a–b (1; 2).
Tersilochinae:	<i>Allophrys</i> sp. a–c (5; 1; 2), <i>Diaparsis</i> sp. a (1), ? <i>Probles</i> sp. a (1).
Phrudinae:	<i>Phrudus</i> sp. a (2).
Mesochorinae:	<i>Mesochorus</i> sp. a–f (2; 1; 8; 1; 1; 1), <i>Stictopisthus</i> sp. a–g (11; 1; 2; 2; 2; 1; 1).
Orthocentrinae:	<i>Chilocyrtus</i> sp. a (1), <i>Megastylus</i> sp. a (1), <i>Neurateles</i> sp. a–b (7; 1), <i>Orthocentrus</i> sp. a–n (3; 3; 1; 2; 1; 1; 7; 1; 2; 1; 1; 2; 2), <i>Plectiscus</i> sp. a–i (6; 1; 13; 1; 4; 3; 4; 2; 1), ? <i>Symplecis</i> sp. a (1), Gen. sp. a (1).
Metopiinae:	<i>Exochus</i> sp. a–b (3; 1), <i>Hypsicera</i> sp. a–c (2; 2; 1), ? <i>Hypsicera</i> sp. d (1), <i>Triclistus</i> sp. a (1), <i>Trieces</i> sp. a–c (1; 1; 1).

APPENDIX 2. Night fog samples from primary rain forest in the Kinabalu NP

In our previous paper (Horstmann *et al.* 1999) only three night fogs could be analyzed, therefore the results were preliminary. Eleven more trees were fogged at night (at about 23:00 h) in primary rain forest in the period 27–30 March 1998. Fogging samples were taken from nine tree species altogether: *Aporosa lagenocarpa*, *A. maingayi*, *A. subcaudata* (Euphorbiaceae), *Barringtonia scortechiniii* (Euphorbiaceae), *Dacryodes laxa* (Burceraceae), *Depressa nervosum* (Gutiferaceae), *Ficus leptogra* (Moraceae), *Ochanostachys amentacea* (Olacaceae) and *Palaquium rostratum* (Sapotaceae). Most Arthropoda taxa were slightly more abundant at night than in daytime (Table 1). Ichneumonidae were more abundant at night by a factor of 1.4 (difference not significant because of the high variability of abundance data), and the individuals were larger by a factor of 1.4 (Mann-Whitney U-test, $P < 0.001$). The subfamily composition of Ichneumonidae in the night fog samples was different in different years. Night fog samples collected in spring 1996 were similar to day fog samples collected at the same time, the subfamilies Cryptinae and Orthocentrinae being most abundant (Horstmann *et al.* 1999). In contrast, night fog samples collected in spring 1998 (59 individuals) differed from the other night fog samples in containing relatively few Cryptinae and Orthocentrinae and more specimens from other subfamilies (2 x 3 table Chi²-test, $P < 0.001$): Pimplinae 23.7 %, Cryptinae 20.3 %, Campopleginae 16.9 %, Metopiinae 15.3 %, Orthocentrinae 3.4 %. The values for α -diversity did not differ noticeably between day and night fog samples (Table 3). All day fog samples (52 samples, 159 species) and all night fog samples (14 samples, 79 species) from primary forest had 18 species in common and Sørensen's index for both series amounted to 0.15.
