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Effects of deforestation on mutualistic interactions of ants with plants and hemipterans in tropical rainforest of Borneo

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Abstract. We examined the effects of slash-and-burn deforestation on the properties of the ant-associated mutualistic interactions with plants and hemipterans in and around a lowland tropical rainforest in Borneo. We compared the frequency of occurrence and composition of the involved species among primary and secondary forest plots of different stand ages (time since last slash-and-burn event). For ants attending both extrafloral nectaries (EFNs) and hemipterans, for trees bearing EFNs, and for trees with hemipteran-attending ants, the number of species was higher in primary than in secondary forest, and less than 20% of species observed in the primary forest plots were also recorded in the secondary forest. For *Macaranga* myrmecophytes, both the number of species and the frequency of occurrence were higher in primary than in secondary forest, and the species observed in secondary forest comprised approximately one-third of the species occurring in primary forest. In contrast the weaver ant *Oecophylla smaragdina*, which tended to exclude other arboreal ant species, was significantly more abundant in secondary than in primary forest. These results suggest that slash-and-burn deforestation drastically decreases the diversity of species involved in mutualistic interactions between ants and plants and between ants and hemipterans.

Keywords: human disturbance through slash-and-burn; ant-plant interaction; ant-hemipteran trophobioses; *Macaranga* myrmecophytes; *Oecophylla smaragdina*; EFN-bearing plants

INTRODUCTION

The area of tropical primary rainforest has rapidly decreased through deforestation by humans, resulting in the creation of several types of secondary forest (Myers 1980, 1989). This decrease is accompanied by a dramatic loss of species richness in some regions (Myers 1988). In particular, lowland tropical rainforests of Southeast Asia are being destroyed at higher rates than those of other tropical regions, and their biodiversity is being lost at a dramatic rate (Sodhi *et al.* 2004). To date, deforestation-related effects of humans on tropical rainforest biodiversity have been evaluated only by determining species losses caused by deforestation (Lawton *et al.* 1998; Liow *et al.* 2001). Some previous studies have attempted to determine species losses by comparing the species richness of select taxonomic groups among forests at different stages of succession or at different elapsed times after deforestation (e.g. Levings & Windsor 1985; Lawton *et al.* 1998; Dunn 2004). To better understand the effects of deforestation on biodiversity, however, not only effects on species richness, but also those on interspecific interactions within a biological community, must be explored because interspecific interactions are likely to be involved in the processes and mechanisms that allow species coexistence in the community. Therefore, it is important to clarify differences in the properties of interspecific interactions, as well as those in species richness, in relation to the degree of deforestation.

Ants have often been used as indicators of the effects of forest disturbance on biodiversity (Belshaw & Bolton 1993; King *et al.* 1998; Vasconcelos 1999; Watt *et al.* 2002; Brühl *et al.* 2003; Bickel *et al.* 2006) because they dominate the ground and arboreal arthropod fauna in tropical forests (Stork 1988; Belshaw & Bolton 1993; Floren & Linsenmair 1997) and are considered to contribute to local species richness through their involvement in various types of interactions, including mutualistic interactions with a wide taxonomic range of organisms. Ant-plants (myrmecophytes), plants with extrafloral nectaries (EFNs), and honeydew-producing hemipterans are common mutualists of ants in the tropics (Buckley 1982; Hölldobler & Wilson 1990; Oliveira & Oliveira-Filho 1991; Koptur 1992; Davidson & McKey 1993; Davidson 1998). Myrmecophytes and plants with EFNs provide food for ants and are defended from herbivory (Beattie 1985; Huxley & Cutler 1991; Oliveira 1997), and hemipterans which offer sugary secretions are defended from predation (Way 1963; Buckley 1987). Myrmecophytes also provide their ant partners with nest sites. These types of mutualistic interactions are ubiquitous in tropical rainforests (Way 1963; Hölldobler & Wilson 1990; Oliveira & Oliveira-Filho 1991; Davidson & McKey 1993; Fiala & Linsenmair 1995; Davidson 1997; Blüthgen *et al.* 2006). Some myrmecophytes such as *Macaranga* spp. are considered to be pioneer trees which grow fast in disturbed areas and hence may function as "sunshade" for seedlings of other tree species that are intolerant of strong sunlight and dryness.

What effect does deforestation have on such mutualistic interactions? To date, few studies have addressed this question by focusing on changes in the properties of ant-associated mutualistic interactions caused by deforestation (e.g. Bruna *et al.* 2005), although some studies have attempted to estimate the effects of deforestation on biodiversity by measuring the species loss of ants (Belshaw & Bolton 1993; Watt *et al.* 2002; Brühl *et al.* 2003). The main purpose of this study was to describe how the properties of ant-associated mutualistic interactions differ among forests of different stand ages (i.e. time since last slash-and-burn event) in a given locality. For this purpose, we measured the frequency of occurrence and composition of species involved in mutualistic interactions between ants and plants or hemipterans in primary and secondary forest plots differing in stand age. By comparing these parameters among forest plots, we attempted to examine the effects of deforestation on the interactions of ants with plants and hemipterans in tropical rainforests.

METHODS

Study sites

The study was conducted from August to September 2003 in primary forest in Lambir Hills National Park and in secondary forest around the outside of the park (4°2' - 4°11'N, 113°50' - 114°3'E; 60 m in altitude; Fig. 1). The park is located about 10 km inland from the coast in the northern part of Sarawak, Malaysia, and covers an area of approximately 69.5 km^2 (Yumoto & Nakashizuka 2005). The climate is humid-tropical, with a weak seasonal change in rainfall (Kato *et al.* 1995; Itioka & Yamauti 2004). Most of the park comprises primary evergreen forest, the majority of which is classified as lowland mixed dipterocarp forest formed on nutrient-poor sandy or clay soil (Watson 1985). The park is surrounded by secondary forest of differing stand age, slash-and-burn fields for cultivation, rice paddy fields, and plantations of rubber or oil palm.

We chose 15 secondary forest plots of three stand types for our survey: four of one-year-old secondary forest stands (abbreviated as 1SF), five of five-year-old secondary forest stands (5SF), and six of old secondary forest stands (>19 years old; OSF). The ages of these forest stands refer to the time since the abandonment of shifting cultivation, in which dry-paddy rice was cultivated for one or two years after slashing, felling and burning all the vegetation there. In 1SF, sedges (Cyperaceae) grew thickly, mixed with small *Macaranga* and *Artocarpus* trees. The term "secondary forest" is valid because the trees are capable of reaching a height of 5 m and a canopy cover of 10% in situ (Convention on Biological Diversity 2007). In 5SF and OSF, the single-layered canopy ranged from 10 to 20 m above the ground. The dominant trees in 5SF and OSF were *Vitex pinnata* (Verbenaceae) and *Artocarpus elasticus* (Moraceae). These forest plots were located 0.5–3 km from the primary forest of the national park and were mostly separated from each other by cultivated fields, plantations, and non-target secondary forest stands (Fig. 1). Several were adjacent to each other. The area of these stands varied from 2772 m^2 to 4917 m^2. One study plot of 100 x 10 m was established at or near the centre in each of the 15 secondary forest stands (Fig. 2a).

In the primary mixed dipterocarp forest of the park, four study plots were set up in the same way as in the secondary forest stands (Fig. 2a). Most of the forest floor inside the four plots was relatively shady with a thick canopy layer, and no obvious forest gaps were included in the plots. We selected two gaps of approximately 10 m in diameter near the four shaded plots. Then, the 2 m-wide fringes of the gaps were set in the additional study plots for gaps in the primary forest (Fig. 2b). Hereafter, the forest stand type in which the four shaded plots were placed is termed "shady area in the primary forest" (SPF), and the forest stand type in which the two additional plots were placed is termed "gap in the primary forest" (GPF).

The average canopy openness, which is related to the light intensity, was estimated from ten photos taken at 1.5 m height with a fisheye lens in each plot (see Nakagawa 2006 for details of the method). Openness was highest in 1SF (20.5% ± 1.9%, mean ± 1 SE), followed by 5SF (9.8% ± 0.3%), GPF (8.8% ± 0.8%), OSF (8.2% ± 0.2%), and SPF (7.3% ± 0.2%).

Field census and sampling

We conducted a field census of ants attending EFNs or hemipterans, as well as of myrmecophytes, in each study plot. Except for GPF plots, each 100 x 10 m plot was divided into 40 subplots of 25 m^2 (Fig. 2a). From each of the subplots, we randomly selected 10 tree saplings or young trees that were 0.5-2 m in height. Where fewer than ten trees occurred in a subplot, we selected supplementary trees from an area adjacent to the subplot, such that a total of 400 trees were selected for each study plot. From each GPF plot, we randomly selected 400 tree saplings or shrub trees of 0.5-2 m in height. In several plots, the total number of census trees was between 400 and 410 because of miscounts.

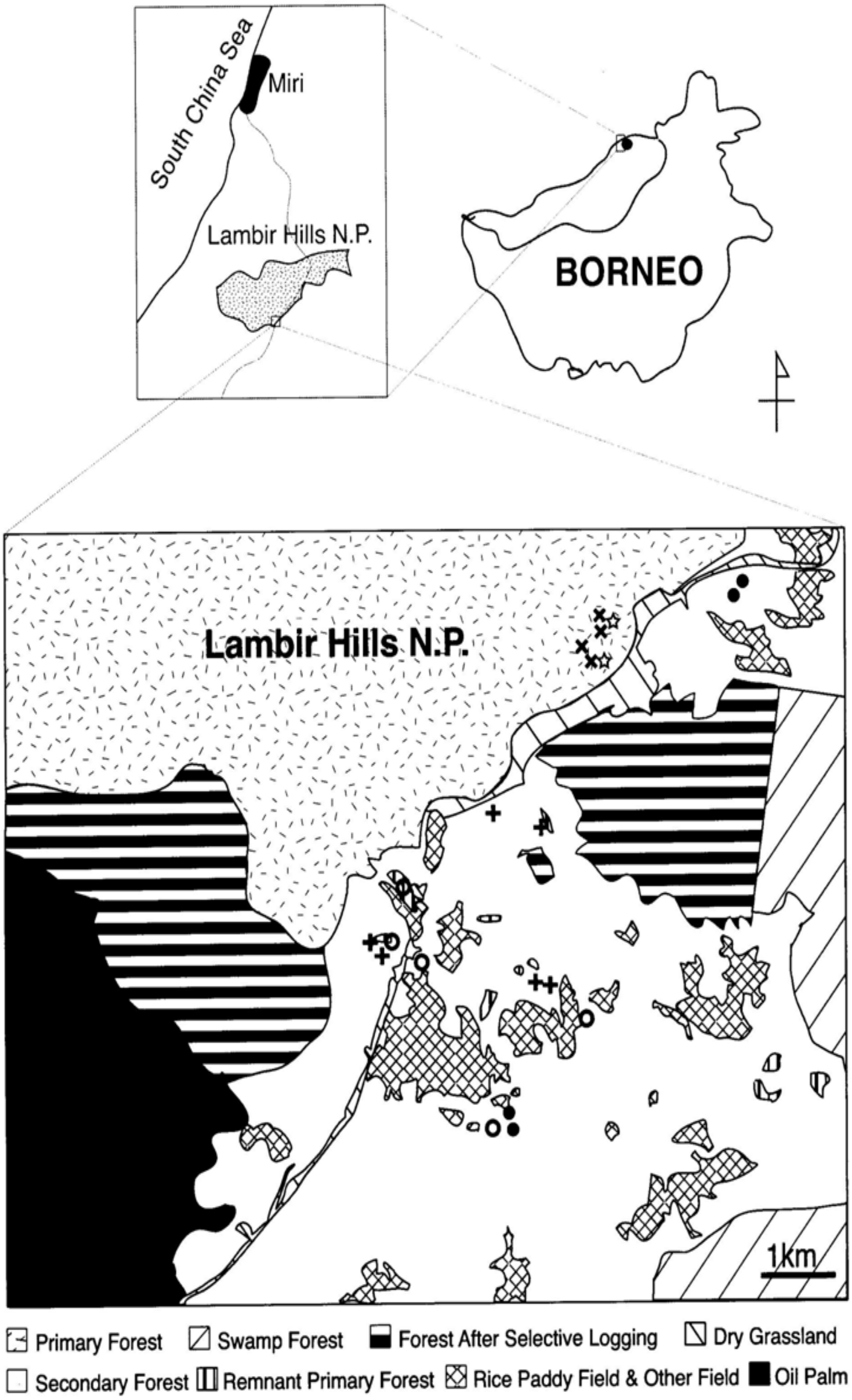

Fig. 1. Location of Lambir Hills National Park and study sites in five forest stand types: 1-year-old secondary forest stand (1SF, closed circle), 5-year-old secondary forest stand (5SF, open circle), >19-year-old secondary forest stand (OSF, vertical cross), forest stands of shady areas in primary forest (SPF, diagonal cross), and gaps in primary forest (GPF, star).

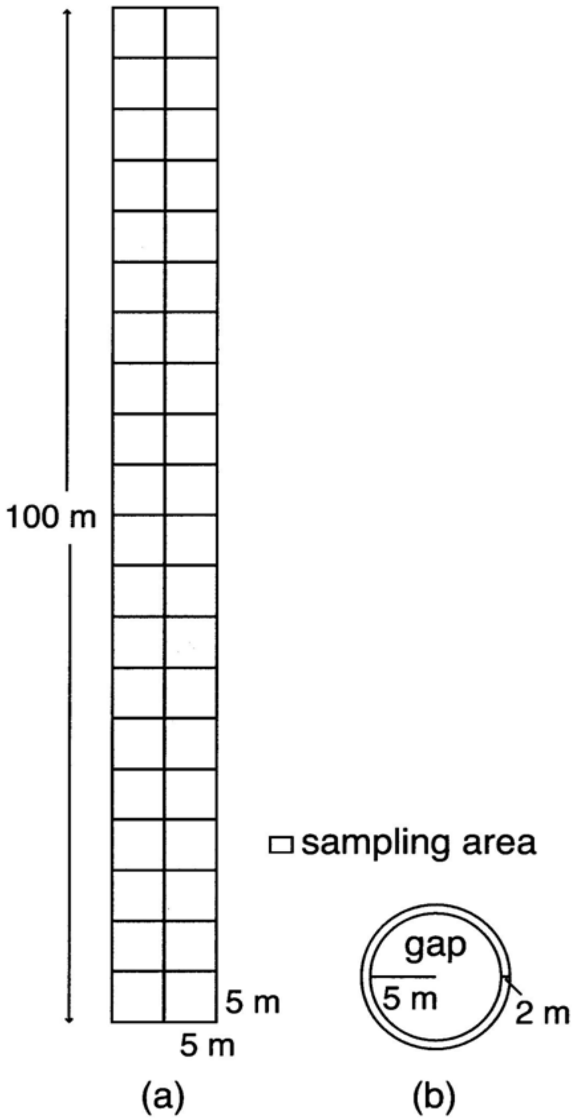

Fig. 2. Types of study plots; (a) 1SF, 5SF, OSF, and SPF plots, (b) GPF plots (see Fig. 1 for abbreviations).

During census events, we checked whether ants attended EFN glands or hemipterans on the selected trees. Lianas were omitted from the census because it was difficult to identify them. When we were unable to find any ants attending hemipterans or EFNs on a tree, we assumed that no mutualistic interactions between ants and plants via EFNs or between ants and hemipterans occurred on that tree. Thus, EFNs and hemipterans that were not attended by ants were omitted from our census. We also checked whether the selected trees were myrmecophytes by searching for domatium-like structures that ants could inhabit, the presence of any entrance and exit holes for ants, and the recruitment of ant symbionts in response to tree-shaking by hand. Myrmecophyte trees in the genus *Macaranga*, which are associated with symbiotic ants often in a highly species-specific manner (Maschwitz *et al*. 1996; Fiala *et al*. 1999; Itino *et al*. 2001; Quek *et al.* 2004), were the only myrmecophytes we found.

All ants found attending EFNs or hemipterans were collected and stored in vials with 80% alcohol. Approximately half of collected ants were identified to named species but the remaining half were assigned to morphospecies by the second author, S. Yamane. All EFN-bearing trees, i.e. trees on which ants attended the EFN glands, and all trees with hemipteran-attending ants were identified by the fourth author, K. Momose. We did not consider the diversity of hemipterans involved in the observed mutualistic interactions because we were unable to collect all hemipterans attended by ants, due to their fast movements. Voucher specimens of the sampled tree species are kept in the Forest Research Center (FRC) of Sarawak Forestry Corporation, and voucher specimens of the sampled ant species are to be deposited in FRC although they are temporarily kept by S. Yamane and H. O. Tanaka.

DATA ANALYSIS

Frequency was defined as the percentage, of all sampled trees (c. 400) in a plot, on which a given association was recorded. We compared the frequencies of EFN-bearing trees where EFNs were attended by ants, trees with hemipteran - attending ants, and myrmecophytes, among the five types of forest stands (1SF, 5SF, OSF, SPF, and GPF), using a G-test. We also calculated the average numbers of species of EFN-attending ants, hemipteran-attending ants, trees that harboured such interactions, and myrmecophytes in each forest stand type. To avoid the complicated interpretation of the results, all *Macaranga* myrmecophytic species and symbiont ant species were omitted from the calculations of frequency and species number for the other kinds of association, although some of the myrmecophytes have EFNs and symbiont ants attend them.

In addition to comparisons among forest stands of different ages, to assess the inferred effect of deforestation on ant-associated interactions, we calculated the above variables for each of primary forest and secondary vegetation in their entirety. To estimate the properties of ant-associated interactions in the whole primary forest (PF), we combined the data from two forest stand types, GPF and SPF. The proportion of the total areas of plots for the two forest stand types were unlikely to be so different from the proportion of shaded area and gap area in the whole primary forest (gaps were estimated to account for 5 to 10 % of the whole primary forest in the study site: unpublished data). Hence, we regarded the data combining as appropriate for getting representative properties of the whole primary forest. To estimate the properties in the whole secondary forest (SF), we combined the data from the three secondary-forest stand types: 1SF, 5SF, and OSF. Although it was virtually impossible to estimate the strict proportion of the three forest types in the whole secondary forest, we here assumed that the proportion of the numbers of plots for the three forest stand types might approximate the proportion of the areas of the different forest stands in the secondary forest. This assumption seems appropriate as the whole secondary forest in the study region consisted of a fine mosaic of the three types of forest stands. We then calculated the frequencies of EFN-bearing trees, trees with hemipteran-attending ants, and myrmecophytes for each of PF and SF and compared the frequencies between SF and PF using a *G*-test.

We also calculated the average number of species of EFN-attending ants, hemipteran-attending ants, trees that harboured such interactions, and myrmecophytes for both forest types and then examined the overlap in species of EFN-attending ants, hemipteran-attending ants, trees that harboured such interactions, and myrmecophytes observed between SF and PF.

We paid specific attention to the frequency of the arboreal weaver ant *Oecophylla smaragdina* (Fabricius) (Formicinae) for the following three reasons. First, *O. smaragdina* often has trophobiotic interactions with hemipterans, and sometimes takes a number of scale insects into its nests (Hölldobler & Wilson 1990; Blüthgen & Fiedler 2002). Second, *O. smaragdina*, which is a polydomous and arboreal species, maintains large exclusive territories around arboreal nests located on multiple trees and the forest floor. It is a dominant omnivorous species which excludes other ants from EFNs and hemipterans. Finally, *O. smaragdina* was one of the most abundant species that often aggregated on trees in the study site, particularly in secondary forest.

RESULTS

EFN-bearing trees

Thirty-one ant species from 12 genera were found to attend EFNs in our study plots. These ants were associated with 17 tree species (nine families). The frequency of trees where EFNs were attended by ants differed significantly among forest stand types (*G*-test: G = 180.05, *P* < 0.001; Fig. 3a). The mean frequencies of EFN-bearing trees were conspicuously higher in GPF and 1SF than in 5SF, OSF, and SPF, in each of which they were <0.5%. However, the mean frequency of EFN-bearing trees did not differ between PF and SF (*G*-test: G = 1.02, *P* = 0.3).

The average number of ant species attending EFNs per plot in PF (3.67 ± 2.04 species per plot) was higher than that in SF (1.27 ± 0.7; Fig. 4a). The average number of ant species was highest in GPF (10 ± 1) and second-highest in 1SF (4.25 ± 2.1). For each of 5SF, OSF, and SPF, only 0.17 to 0.5 species of ants were observed attending EFNs on average. No single ant species was observed to attend EFNs in both PF and SF (Fig. 4a; Appendix 1).

The average number of species of EFN-bearing trees per plot in PF (2.67 ± 2.04) was higher than that in SF (0.4 ± 0.16, Fig. 4b). The average number of species of EFN-bearing trees was highest in GPF (7). In the other forest stand types, only 0.17 to 1 species of EFN-bearing trees per plot were found. Of all the species of EFN-bearing trees that were observed in PF, only 13% were also observed in SF (Fig. 4b, Appendix 2). In 1SF, 96% of all 52 individuals of EFN-bearing trees observed belonged to one species, *Homalanthus populneus* (Geiseler) (Euphorbiaceae), and most trees were attended by two ant species, *Crematogaster* sp. 85 (Myrmicinae) and *Tapinoma* sp. 1 (Dolichoderinae, see Appendix 1, 2).

Trees with honeydew-producing hemipterans

Twenty ant species from eight genera were found to be associated with hemipterans at our study plots. These trophobioses were found on at least 23 host tree species (14 families). The frequency of trees on which hemipterans were attended by ants differed significantly among forest stand types (*G*-test, G = 48.01, *P* < 0.001; Fig. 3b). The mean frequencies in 5SF, GPF, and SPF ranged from 1.48% to 2.58%, whereas those in OSF and 1SF were <0.65%. The mean frequency did not differ between PF and SF (*G*-test, G = 1.59, *P* = 0.2).

The average number of ant species attending hemipterans per plot in PF (3.5 ± 0.72) was higher than that in SF (0.93 ± 0.28, Fig. 4c). The average number of ant species was highest in GPF (4 ± 1) and second-highest in SPF (3.25 ± 1.03). For each of 1SF, 5SF, and OSF, 0.75 to 1.17 species of ants were observed attending hemipterans in average. Of all the species of ant that were observed in PF, only 19% were observed in SF (Fig. 4c, Appendix 3).

The average number of tree species on which hemipterans were attended by ants per plot in PF

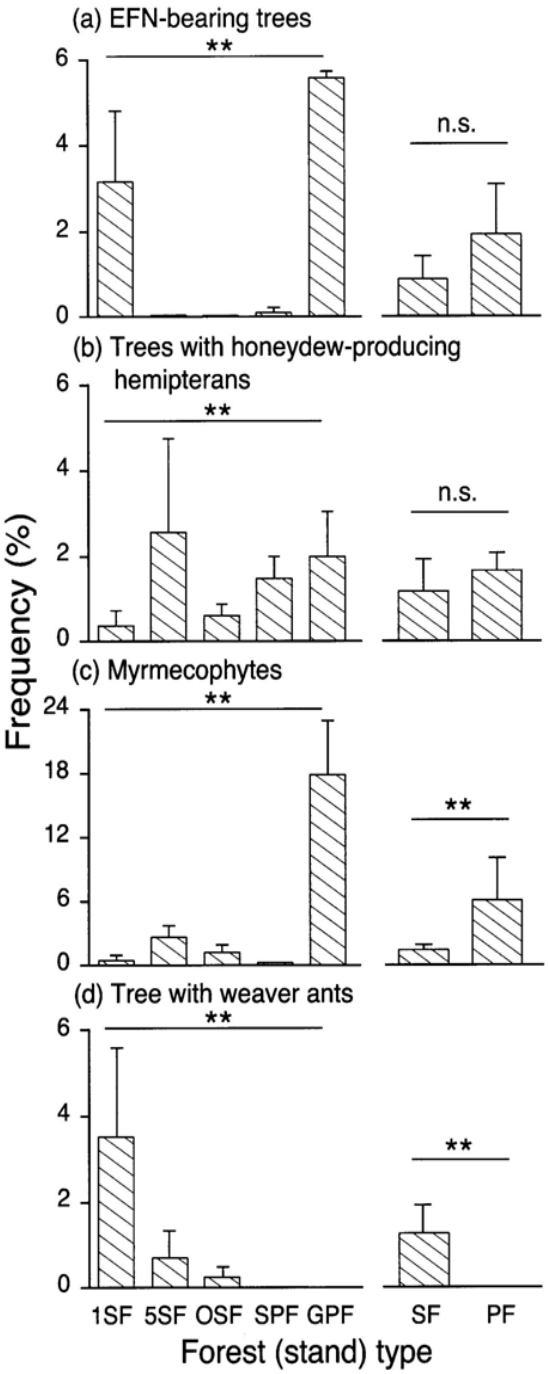

Fig. 3. Frequency of (a) trees with extrafloral nectaries (EFNs) attended by ants, (b) trees with ant-tended hemipterans, (c) myrmecophytic trees, and (d) trees with weaver ants Oecophylla smaragdina in five forest stand types (see Fig. 1 for abbreviations), and in all plots of secondary forest (SF) and primary forest (PF). The frequency was defined as the percentage, of all sampled trees (c. 400) in a plot, on which a given association was recorded. Bars and vertical lines indicate means and 1 SE, respectively. **There were significant differences in the frequency among five forest stand types (*G*-test, $P < 0.001$) and between SF and PF (*G*-test, $P < 0.001$).

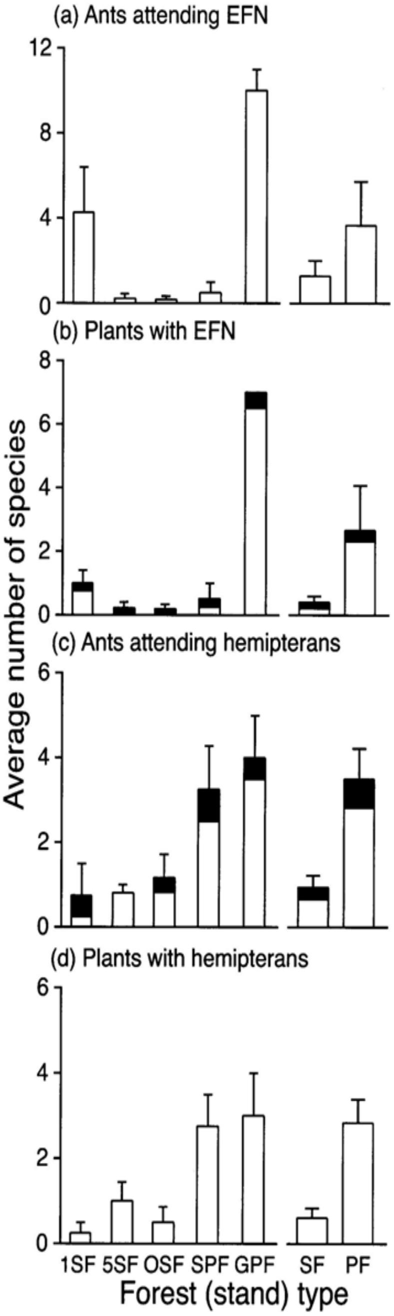

Fig. 4. Average number of species of (a) ants attending extrafloral nectaries (EFNs), (b) EFN-bearing trees (trees on which ants attended the EFN glands), (c) ants attending hemipterans, and (d) trees with hemipterans attended by ants in five forest stand types (see Fig. 1 for abbreviations), and in all plots of secondary forest (SF) and primary forest (PF). Bars indicate the average number of species; solid areas within the bars indicate the average number of plant and ant species observed in both PF and SF. PF and SF shared no ant species that were observed attending EFNs, and no tree species that were observed harbouring hemipterans attended by ants.

(2.83 ± 0.54) was higher than that in SF (0.6 ± 0.21; Fig. 4d). The average number of tree species was highest in GPF (3 ± 1) and second-highest in SPF (2.75 ± 0.75). In each of the three types of secondary forest stands, fewer tree species were found per plot than in any type of primary forest stands. No tree species on which hemipterans were attended by ants was observed in PF and SF (Fig. 4d; Appendix 4). In 5SF, *Melastoma malabathricum* (Melastomataceae) accounted for about 89% of all 53 tree individuals with hemipterans that were attended by ants of one species, *Dolichoderus affinis* (Dolichoderinae), which was also observed on other trees (Appendix 3, 4).

Myrmecophytes

All ten species of myrmecophytic trees found belonged to the genus *Macaranga* (Euphorbiaceae) (Appendix 5). The frequency of myrmecophytes differed significantly among forest stand types (*G*-test, G = 248.55, *P* < 0.001; Fig. 3c). The frequency was higher in GPF than in any other forest stand type, and was about seven times higher than that in 5SF, which had the second-highest frequency. The frequencies in OSF, 1SF, and SPF were less than half, less than one-fourth, and about one-ninth of the frequency in 5SF, respectively. The total frequency of *Macaranga* myrmecophytes in PF was significantly higher than that in SF (*G*-test, G = 23.80, *P* < 0.001).

The average number of myrmecophytic *Macaranga* per plot in PF (3.17 ± 1.56) was higher than that in SF (1.07 ± 0.25, Fig. 5). The average number of species of myrmecophytic *Macaranga* was highest in GPF (8). In the other forest stand types, only 0.75 to 1.6 species of myrmecophytic *Macaranga* per plot were found. All *Macaranga* myrmecophyte species observed in SF were also found in PF. In 5SF, *Macaranga bancana* accounted for 89% of 56 *Macaranga* individuals (Appendix 5). The occurrence of this species was higher in SF (82 individuals) than in PF (24 individuals).

Trees with weaver ants

The frequency of trees occupied by *O. smaragdina* differed significantly among forest stand types (*G*-test, G = 126.06, *P* < 0.001; Fig. 3d). The frequency was notably higher in 1SF (3.5% ± 2.1%) than in the other forest stand types (5SF: 0.7% ± 0.6%, OSF: 0.3% ± 0.3%, SPF: 0%, GPF: 0.002% ± 0.002%) and tended to decrease as stand age increased. The total frequency of trees occupied by *O. smaragdina* in SF was significantly higher than that in PF (*G*-test, G = 36.97, *P* < 0.001).

DISCUSSION

The scope of our field census was restricted to the lowest foliage layer of forests, where mainly seedlings of canopy trees and pioneer trees develop leaves. Hence, the status of ant-associated mutualistic interactions in the canopy was not reflected in our data. Nevertheless, it is meaningful to compare the properties of ant-associated interactions among forest stand types based on our data. The species composition of arboreal ants differs between the canopy layer and the lower-tree layer (arboreal space just above the ground), and is specific to each layer in Bornean rainforests (Brühl *et al.* 1998). Thus, we discuss our results based on the assumption that the species composition of arboreal ants in the lower tree layer is independent from that in the canopy. Even if this assumption is not strictly true, our results provide necessary information for considering the growth and survival of tree seedlings, which may be affected by the properties of ant-associated mutualistic interactions in the lower-tree layer as removal of herbivores by ants is important for survival of the seedlings.

To estimate the species diversity of the whole primary forest, the data from the two types of habitats in the primary forest, gaps and shady forest floor, were grouped together because both habitats are important components that characterise primary forests (Whitmore 1990). In contrast, we did not establish plots in and around gaps in the secondary forests because of the scarcity of gaps. Thus, for estimating species diversity in secondary forest as a whole, the data

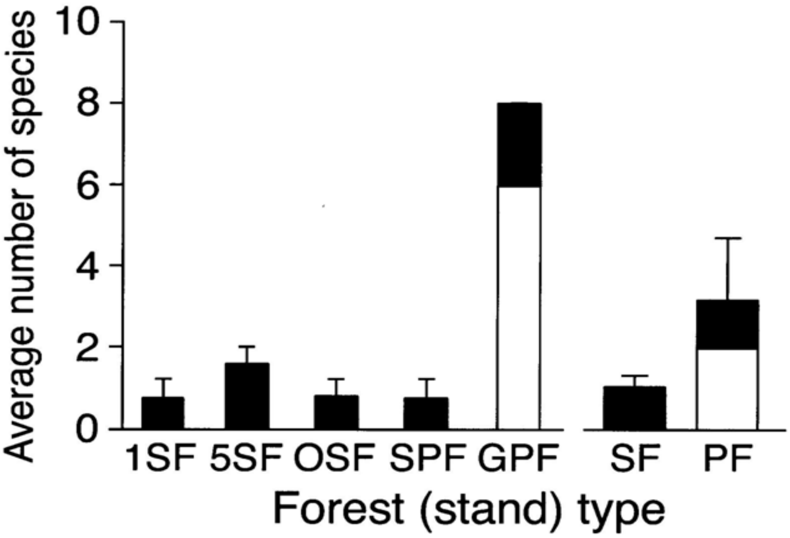

Fig. 5. Average number of *Macaranga* myrmecophyte species in five forest stand types (see Fig. 1 for abbreviations), and in all plots of secondary forest (SF) and primary forest (PF). Bars indicate the average number of species; solid areas within the bars indicate the average number of species observed in both PF and SF.

from all studied plots of secondary forest differing in stand age were grouped together without conducting census in gaps there.

Our results demonstrate that slash-and-burn deforestation affects the properties of ant-associated mutualistic interactions, such as ant–plant interactions via EFNs and myrmecophytism, and ant–hemipteran interactions. We observed dramatic decreases in the diversity of species involved in these mutualistic interactions, and the reduced frequency of myrmecophytic trees in secondary forest is likely a lasting effect of deforestation. We found that deforestation simplified the composition of the involved species. We also noticed there was low overlap in species composition between secondary and primary forest. Although all the PF plots were concentrated in a narrow area compared to SF plots, they seem not to be pseudoreplicated, because the overlap in ant species composition between any two PF plots was low; in SPFs 73% of all the ant species in target associations, and 93% of the plant species, were observed in only one plot. Overlap was also low between the two GPFs; only 12% of all the ants and 16% of the plants were observed in both plots. Interestingly, the overlap in ant and plant species between SPF and GPF plots was also low; only 2.9% of all the ant species and 9.8% of all the plant species that were observed in SPFs or GPFs were observed in both types of stand.

Because we were unable to sample all hemipterans, mainly membracids and cicadellids, that were observed being attended by ants, we did not analyse their species diversity. However, similar to the other organisms involved, the number of hemipteran species observed appeared to be much lower in secondary than in primary forest; at least ten species of ant-tended hemipterans were observed in the primary forest, whereas at most seven species were observed in the secondary forest (H.O. Tanaka, personal observation). In both forests, the hemipterans were mainly membracids. Moreover, in the 5-year-old secondary forest stands, a trophobiosis between *Dolichoderus affinis* Emery and a membracid species was remarkably predominant.

Differences in the numbers of ant and plant species involved in mutualistic interactions among the three secondary forest stand types, and differences in their frequencies of occurrence, suggest that the effects of deforestation may persist, even after 20 years, during which time trees are expected to have grown to more than 20 m in height. The relatively impoverished tree flora and lack of gaps may be causal factors that suppress the occurrence of ant-associated mutualistic interactions in secondary forest.

The frequency of EFN-mediated ant–plant interactions, and the diversity of the associated ant species, were both second-highest in 1-year-old secondary forest stands among the five forest stand types. The light intensity was strongest in 1-year-old secondary forest stands, suggesting that EFN-mediated ant–plant interactions may be enhanced by strong light conditions. Generally, in sunny conditions, trees tend to grow more rapidly and produce more new leaves. We might infer that the number and production of EFNs is higher in sunny than in shady habitats because EFNs tend to be more available on young than on old leaves (Heil *et al*. 2000). Consequently, EFN-mediated ant–plant interactions would frequently occur in such sunny habitats. However, this inference is not supported by the fact that the light intensity as represented by canopy openness in the forest gap of primary forest, where both frequencies and diversity of the involved species were highest, was most similar to that in the forest floor of old secondary forest stands, where both parameters were lowest.

There is a possibility that EFN-mediated ant–plant interactions occur relatively frequently in the canopy, even in old secondary forest stands. However, the frequency of ants attending EFNs in the canopy of primary forest appeared to be much lower than that observed in the gaps (H.O. Tanaka, personal observation). The status of EFN-mediated ant–plant interactions in the canopy, especially in secondary forest, remains to be examined in future studies.

Myrmecophytism between *Macaranga* and ant symbionts is considered to be a highly species-specific, coevolved symbiotic mutualism (Fiala *et al.* 1999; Itino *et al.* 2001; Quek *et al.* 2004). Deforestation may impose severe effects, especially on highly species-specific symbiotic systems, such as *Macaranga* myrmecophytism. Although light conditions have been considered important in affecting the growth, spatial distribution, and habitat use of *Macaranga* species, including those found here (Davies 1998; Davies *et al.* 1998), the observed frequency and diversity of *Macaranga* species in relation to light conditions suggest that suitable light conditions alone are not sufficient for occurrence of diverse species. In general, the relative density of *Macaranga* trees has been presumed to be higher in secondary forests than in primary forests, since many *Macaranga* species are pioneer trees (Whitmore 1969). However, the results of this study contradict the presumption. The contradiction may be due to the relatively low density of myrmecophytic species in the secondary forest in this study; the density of myrmecophytic species was notably higher in the gap in the primary forest (T. Itioka, personal observation). By contrast, in the secondary forest, the number of individuals of non-myrmecophytic *Macaranga* species, mainly *Macaranga gigantea* (Reich. F & Zoll.), was much higher than that of the common myrmecophytic *Macaranga* species.

The decreasing frequency of the weaver ant *O. smaragdina* with increased stand age and its absence from primary forest, including the canopy (H.O. Tanaka, personal observation), suggest that this species prefers disturbed areas and that deforestation is advantageous to this species. Considering its dominance in secondary forest and the large size of its territories, it is possible that this species suppresses the activity of other ant species that have mutualistic interactions with plants or hemipterans. Whether *O. smaragdina* competes with other ant species, how this ant interacts with hemipterans, and what effect the attended hemipterans have on host plants remain important questions to be explored.

We did not consider the effects of forest size. Although the size effect should be examined in the future, it was probably insignificant here because most of the studied secondary forest stands were located within a mosaic of various forest stand types. These could mitigate size effects because total area of the secondary forest including the studied forest stands was large. As well as size effects, distance effects, i.e. effects that are imposed by distance from the primary forest on some traits of the target forest stands, remain to be studied.

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Appendix 1 List of ant species attending EFNs in five forest stand types. 1SF, 1-year-old secondary forest stand; 5SF, 5-year-old secondary forest stand; OSF, >19-year-old secondary forest stand; SPF, forest stand of shady areas in primary forest; GPF, forest stand of gaps in primary forest. All *Macaranga* symbiont ant species are omitted from this list. Figures show the number of trees where EFNs were attended by the ants. Undescribed species were classified to morphospecies by S. Yamane (designated SKY) or H. O. Tanaka (HOT), who have retained the voucher specimens.

		FOREST STAND TYPE				
ANTS		1SF	5SF	OSF	SPF	GPF
PONERINAE	*Pachycondyla* sp. 28 of SKY					1
MYRMICINAE	*Cardiocondyla wroughtonii* (Forel)	3				
	Crematogaster decamera Forel					1
	Crematogaster modiglianii Emery				1	
	Crematogaster spengeli Forel					1
	Crematogaster sp. 5 of SKY	7				
	Crematogaster sp. 10 of SKY					1
	Crematogaster sp. 26 of SKY	1				
	Crematogaster sp. 52 of SKY			1		
	Crematogaster sp. 84 of SKY	1				
	Crematogaster sp. 85 of SKY	12				
	Crematogaster sp. 93 of SKY					1
	Crematogaster sp. 112 of SKY	3				
	Crematogaster sp. C of HOT					2
	Monomorium floricola (Jerdon)	4				
	Pheidole huberi Forel		1			
	Pheidole merimbun Eguchi					1
	Tetramorium palaense Bolton					1
DOLICHODERINAE	*Dolichoderus beccarii* Emery				1	
	Dolichoderus thoracicus (Smith)					1
	Tapinoma sp. 1 of SKY	18				
	Technomyrmex butteli Forel					2
FORMICINAE	*Camponotus reticulatus* Roger	2				
	Camponotus sp. 1 of SKY					3
	Camponotus sp. 29 of SKY					1
	Cladomyrma andrei (Emery)					1*
	Paratrechina opaca (Emery)					3
	Paratrechina sp. 1 of SKY	1				
	Polyrhachis armata (Le Guillou)					1
	Polyrhachis phalerata Menozzi					1
	Polyrhachis sp. 142 of SKY					1

* *Cladomyrma andrei* is known to be a plant-ant species which inhabits in particular myrmecophytic species such as *Spatholobus*. However, we collected more than three workers of the ant species when they were attending EFNs on a tree of non-myrmecophytic *Mallotus leucodermis.* We did not confirm their nest sites.

Appendix 2 List of species of EFN-bearing trees (trees on which ants attended the EFN glands) and their occurrence in five forest stand types; 1SF, 5SF, OSF, SPF, GPF (see Appendix 1 for abbreviations). All *Macaranga* myrmecophytic species are omitted from this list.

PLANTS		FOREST STAND TYPE				
		1SF	5SF	OSF	SPF	GPF
DIPTEROCARPACEAE	*Shorea macroptera* Dyer					1
EBENACEAE	*Diospyros nidus-avis* Kosterm.					3
ELAEOCARPACEAE	*Elaeocarpus* sp.					1
EUPHORBIACEAE	*Claoxylon longifolium* (Bl.) Endl. ex Hassk.					2
	Endospermum diadenum (Miq.) Airy Shaw	2				1
	Homalanthus populneus (Geisel.) Pax	50				
	Macaranga gigantea (Rchb. f. & Zoll.) Müll. Arg.					1
	Macaranga praestans Airy Shaw					2
	Mallotus leucodermis Hook. f.					2
	Omphalea bracteata (Blanco) Merr.					2
LOGANIACEAE	*Fagraea racemosa* Jack ex Wall.					1
MELASTOMATACEAE	*Pternandra multiflora* Cogn.					1
RUBIACEAE	*Ixora stenophylla* (Korth.) Kuntze				1	
	Ixora woodii Brem.		1	1	1	
	Tarenna sp.					1
SAURAUIACEAE	*Saurauia glabra* Merr.					3
STERCULIACEAE	*Scaphium longepetiolatum* (Kosterm.) Kosterm.					1

Appendix 3 List of ant species attending honeydew-producing hemipterans and occurrence of the trees with ant-hemipteran associations in five forest stand types; 1SF, 5SF, OSF, SPF, GPF (see Appendix 1 for abbreviations).

		FOREST STAND TYPE				
ANTS		1SF	5SF	OSF	SPF	GPF
PONERINAE	*Pachycondyla* sp. 28 of SKY					1
MYRMICINAE	*Crematogaster coriaria* Mayr				4	
	Crematogaster modiglianii Emery				5	
	Crematogaster spengeli Forel					1
	Crematogaster sp. 5 of SKY	1			1	
	Crematogaster sp. A of HOT	4		1		
	Crematogaster sp. G of HOT	1		4	4	
	Pheidole longipes Smith		2	5		
	Pheidole merimbun Eguchi					1
DOLICHODERINAE	*Dolichoderus affinis* Emery		51	2		
	Dolichoderus beccarii Emery				5	
	Dolichoderus thoracicus (Smith)			2	2	1
	Technomyrmex butteli Forel					1
	Technomyrmex kraepelini Forel				1	
FORMICINAE	*Camponotus rufifemur* Emery				1	
	Camponotus sp. 15 of SKY			1		
	Paratrechina opaca (Emery)					1
	Paratrechina sp. 1 of SKY				2	
	Polyrhachis orsylla Smith complex					1
	Polyrhachis vindex Smith					1

Appendix 4 List of tree species with ant-hemipteran associations and their occurrence in five forest stand types; 1SF, 5SF, OSF, SPF, GPF (see Appendix 1 for abbreviations). Voucher specimens of trees on which honeydew-producing hemipterans were found in one plot of SPF were lost.

		FOREST STAND TYPE				
PLANTS		1SF	5SF	OSF	SPF	GPF
ANNONACEAE	*Dasymaschalon crassiflorum* Merr.				1	
DILLENIACEAE	*Dillenia suffruticosa* (Griff.) Mart.		1			
EUPHORBIACEAE	*Claoxylon longifolium* (Bl.) Endl. ex Hassk.					2
	Homalanthus populneus (Geisel.) Pax	6				
	Macaranga gigantea (Rchb. f. & Zoll.) Müll. Arg.		2			
	Mallotus eucaustus Airy Shaw				1	
	Mallotus leucodermis Hook. f.				1	2
	Tapoides villamilii (Merr.) Airy Shaw				1	
FLACOURTIACEAE	*Hydnocarpus borneensis* Sleum.				2	
LAURACEAE	*Litsea petiolata* Hook. f.		2			
	Litsea rubicunda Kosterm.				1	
LOGANIACEAE	*Fagraea racemosa* Jack ex Wall.			3		
	Fagraea spicata Baker				1	
MELASTOMATACEAE	*Melastoma malabathricum* L.		47			
MORACEAE	*Artocarpus odoratissimus* Blanco				1	
MYRISTICACEAE	*Horsfieldia fragillima* Airy Shaw				2	
MYRTACEAE	*Eugenia acuminatissima* (Blume) Kurz					1
	Syzygium sp.					1
OLACACEAE	*Strombosia ceylanica* Gardner			5		
ROSACEAE	*Prunus beccarii* (Ridley) Kalkman		1			
RUBIACEAE	*Gaertnera vaginans* (DC.) Merr.			7		
	Ixora stenophylla (Korth.) Kuntze				2	
THEACEAE	*Adinandra dumosa* Jack					1
Unidentified*						1

Appendix 5 List of *Macaranga* myrmecophyte species and their occurrence in five forest stand types; 1SF, 5SF, OSF, SPF, GPF (see Appendix 1 for abbreviations). The respective symbiotic ant species based on observations are given in parentheses.

	FOREST STAND TYPE				
Macaranga myrmecophytes	1SF	5SF	OSF	SPF	GPF
Macaranga bancana (Miq.) Müll. Arg. (*Crematogaster borneensis* André)	3	50	29	2	22*
Macaranga beccariana Merr. (*Crematogaster decamera* Forel)		5	1	2	21
Macaranga hosei King ex Hook. f. (*Crematogaster* sp. 4)					4
Macaranga hullettii King ex Hook. f. (*Crematogaster borneensis* André)					3
Macaranga hypoleuca (Rchb. f. & Zoll.) Müll. Arg. (*Crematogaster decamera* Forel)					3
Macaranga umbrosa S. J. Davies** (*Crematogaster* Msp. 3 (Fiala et al. 1999))			1		1
Macaranga lamellata Whitmore (*Camponotus macarangae* Dumpert)					2
Macaranga sp. A (*Crematogaster* sp.***)					4
Macaranga trachyphylla Airy Shaw (*Crematogaster borneensis* André)					5
Macaranga winkleri Pax & K. Hoffm. (*Crematogaster* sp. 2)	7	1		1	

* Of the 22 individuals of *Macaranga bancana* in GPF, 13 individuals appeared to differ from the typical *M. bancana*, were rather similar in morphology to *Macaranga aëtheadenia* because they had a few characteristics of saplings of *M. aëtheadenia*. Considering the difficulty in distinguishing them when individual trees are young, we combined both types of trees together. This gives the under-estimation of number of species in the primary forest, but does not affect the comparison of the frequency of all *Macaranga* species between primary and secondary forests.

** This *Macaranga* species was previously recognized as *M. kingii* var. *platyphylla* in Lambir Hills National Park (e.g., Davies et al. 1998; Fiala et al. 1999). But recently, it has been recognized as *M. umbrosa* (Davies 2001).

*** This *Crematogaster* species, which were observed to inhabit *Macaranga* sp. A, was similar in morphology to *Crematogaster borneensis* associated with *Macaranga trachyphylla*. But it has not yet been clarified whether these are same species or not.