

Effects of Deforestation on Mutualistic Interactions of Ants with Plants and Hemipterans in a Tropical Rain Forest of Borneo

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Introduction

In Southeast Asia, the area of lowland tropical rain forests has decreased rapidly as a result of deforestation by humans, resulting in the creation of several types of secondary forest (Sodhi et al. 2004). This decrease has been accompanied by a dramatic loss of species richness. So far, deforestation-related effects of humans on tropical rain forest biodiversity have been evaluated only by determining the species losses caused by deforestation (e.g., Levings and Windsor 1985; Lawton et al. 1998; Dunn 2004). To better understand the effects of deforestation on biodiversity, however, we must explore not only the effects on species richness, but also those on interspecific interactions within a biological community; interspecific interactions are likely to be involved in the processes and mechanisms that allow species to coexist in the community. Therefore, it is important to clarify differences in the properties of interspecific interactions, as well as differences 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 (e.g., Belshaw and Bolton 1993; Brühl et al. 2003; Bickel et al. 2006) because they dominate the terrestrial and arboreal arthropod fauna of tropical forests (Stork 1988; Belshaw and Bolton 1993; Floren and 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 commonly enter into mutualistic relationships with ants in the tropics (Buckley 1982; Hölldobler and Wilson 1990; Oliveira and Oliveira-Filho 1991; Koptur 1992; Davidson and McKey 1993; Davidson 1998).

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 loss of ant species (e.g., Belshaw and Bolton 1993; Brühl et al. 2003). The main purpose of the present study was thus to describe how the properties of ant-associated mutualistic interactions differ among forests of different stand ages (i.e., different elapsed time since the last slash-and-burn event) in a given locality. For this purpose, we measured the frequency of occurrence and the species composition 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 rain forests.

Methods

The study was conducted from August to September 2003 in a primary forest of the Lambir Hills National Park, Sarawak, Malaysia and in secondary forest of differing stand age around the outside of the park. We chose 15 secondary forest plots of three stand types for our survey: four plots of 1-year-old secondary forest stands (abbreviated as 1SF), five of 5-year-old secondary forest (5SF), and six of old secondary forest (>19 years old; OSF). We established one 100×10 m study plot at or near the center of each of the 15 secondary forest stands. In the park's primary mixed dipterocarp forest, we established four shaded primary forest study plots (SPF) in the same way as in the secondary forest stands. 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 also selected two gaps 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 (GPF) for gaps in the primary forest.

We conducted a field census of ants found attending EFNs, hemipterans, and myrmecophytes in each study plot. Except for the GPF plots, each 100×10 m plot was divided into 40 subplots of 25 m² each. In each subplot, we randomly selected 10 tree saplings or young trees that were 0.5 to 2.0 m in height. In each GPF plot, we randomly selected 400 tree saplings or shrubs 0.5 to 2.0 m in height. In several plots, the total number of census trees ranged between 400 and 410 because of miscounts.

During each census, we checked whether ants were present attending EFN glands or hemipterans on the selected trees. Lianas were omitted from the census because it was difficult to identify them. 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 and for the presence of any entrance and exit holes for ants; in addition, we tested whether ant symbionts had been recruited by manually shaking the trees. We also checked whether the weaver ant *Oecophylla smaragdina* (Fabricius) (Formicinae) was present on the selected trees because this species maintains large territories around arboreal nests located on multiple trees in which it excludes other ants from any EFNs and hemipterans present in the territory (Hölldobler and Wilson 1990; Blüthgen and Fiedler 2002).

We calculated the frequency of each association as the percentage of all sampled trees (ca. 400) in a plot on which a given association was recorded. We compared the frequencies of EFN-bearing trees on which the EFNs were attended by ants, of trees with hemipteran-attending ants, of myrmecophytes, and of trees with *O. smaragdina*, among the five types of forest stand (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 harbored such interactions, and myrmecophytes in each forest type.

In addition to comparisons among forest stands of different ages, we assessed the inferred effect of deforestation on ant-associated interactions by calculating the above-mentioned variables for primary and secondary forest vegetation as separate categories. To estimate the properties of ant-associated interactions for primary forest as a whole (PF), we combined the data from the GPF and SPF forest types. To estimate the properties for the secondary forest as a whole (SF), we combined the data from the three secondary-forest types (1SF, 5SF, and OSF).

Results

The frequency of trees on which EFNs were attended by ants differed significantly among forest stand types ($G = 180.05$, $P < 0.001$). The mean frequencies of EFN-bearing trees attended by ants (3.2 to 5.6%, respectively) were conspicuously higher in GPF and 1SF than in 5SF, OSF, and SPF (<0.5% in each). However, the mean frequency of EFN-bearing trees attended by ants did not differ between PF and SF ($G = 1.02$, $P = 0.30$).

The average number of ant species per plot found attending EFNs in PF (3.7 ± 2.0 species per plot) was higher than that in SF (1.3 ± 0.7). The average number of ant species was highest in GPF (10.0 ± 1.0) and second-highest in 1SF (4.3 ± 2.1). For 5SF, OSF, and SPF, an average of only 0.2 to 0.5 species of ants were observed attending EFNs. No ant species attended EFNs in both PF and SF.

The average number of species of EFN-bearing trees per plot in PF (2.7 ± 2.0) was higher than that in SF (0.4 ± 0.2). The average number of species of EFN-bearing trees was highest in GPF (7.0). In the other forest stand types, only 0.2 to 1.0 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. In 1SF, 96% of all 52 EFN-bearing trees that we observed belonged to one species (*Homalanthus populneus* (Geiseler), Euphorbiaceae), and most trees were attended by one of two ant species: *Crematogaster* sp. 85 (Myrmicinae) and *Tapinoma* sp. 1 (Dolichoderinae).

The frequency of trees on which hemipterans were attended by ants differed significantly among forest stand types ($G = 48.01$, $P < 0.001$). The mean frequencies in 5SF, GPF, and SPF ranged from 1.5 to 2.6%, whereas those in OSF and 1SF were <0.65%. The mean frequency did not differ between PF and SF ($G = 1.59$, $P = 0.20$).

The average number of ant species per plot attending hemipterans in PF (3.5 ± 0.7) was higher than that in SF (0.9 ± 0.3). The average number of ant species was highest in GPF (4.0 ± 1.0) and second-highest in SPF (3.3 ± 1.0). In 1SF, 5SF, and OSF, an average of 0.8 to 1.2 species of ants were observed attending hemipterans. Of all the species of ant that were observed in PF, only 19% were also observed in SF.

The average number of tree species per plot on which hemipterans were attended by ants in PF (2.8 ± 0.5) was higher than that in SF (0.6 ± 0.2). The average number of tree species was highest in GPF (3.0 ± 1.0) and second-highest in SPF (2.8 ± 0.8). In each of the three types of secondary forest stand, fewer tree species were found per plot than in any type of primary forest stand. No tree species on which hemipterans were attended by ants was observed in both PF and SF. In 5SF, *Melastoma malabathricum* (Melastomataceae) accounted for about 89% of the 53 trees with hemipterans that were attended by ants of one species, *Dolichoderus affinis* (Dolichoderinae), which was also observed on other trees.

All 10 species of myrmecophytic trees belonged to the genus *Macaranga* (Euphorbiaceae). The frequency of myrmecophytes differed significantly among forest stand types ($G = 248.55$, $P < 0.001$). The frequency was higher in GPF than in any other forest stand type, and was about seven times the value in 5SF, which had the second-highest frequency. The frequencies in OSF, 1SF, and SPF were less than 7%, 4%, and 2% of the frequency in GPF, respectively. The total frequency of *Macaranga* myrmecophytes in PF was significantly higher (6.2 versus 1.5%) than that in SF ($G = 23.80$, $P < 0.001$).

The average number of myrmecophytic *Macaranga* species per plot in PF (3.2 ± 1.6) was higher than that in SF (1.1 ± 0.3). The average number of species of myrmecophytic *Macaranga* was highest in GPF (8.0). In

the other forest stand types, only 0.8 to 1.6 species of myrmecophytic *Macaranga* per plot were found. All *Macaranga* myrmecophytes observed in SF were also found in PF. In 5SF, *Macaranga bancana* accounted for 89% of the 56 *Macaranga* individuals. The occurrence of this species was higher in SF (82 individuals) than in PF (24 individuals).

The frequency of trees occupied by *O. smaragdina* differed significantly among forest stand types ($G = 126.06$, $P < 0.001$). The frequency was notably higher in 1SF ($3.5\% \pm 2.1\%$) than in the other forest stand types ($0.7\% \pm 0.6\%$ for 5SF, $0.3\% \pm 0.3\%$ for OSF, 0% for SPF, and $<0.01\%$ for GPF) 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 (1.3 vs. $<0.01\%$; $G = 36.97$, $P < 0.001$).

Discussion

Our results demonstrate that slash-and-burn deforestation affects the properties of ant-associated mutualistic interactions. For ants attending both 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 fewer than 20% of the species observed in the primary forest plots were also recorded in the secondary forest plots. 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 *O. 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 ant-associated mutualistic interactions and simplifies the composition of the involved species. We also found that these effects of deforestation lasted for 19 years.

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