

Effects of Canopy Gaps on Ant–Hemiptera–Plant Interactions in Lambir Hills National Park, Sarawak

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Introduction

When a tree dies in a closed-canopy forest, it creates a “canopy gap”, which is the initial stage of a mini-successional sequence called gap-phase regeneration, culminating in the replacement of the original canopy tree by one or more new trees (Hubbell et al. 1999). Over the past few decades, a considerable number of studies have been done on tree species in canopy gaps (Lawton and Putz 1988; Denslow 1995; Hubbell et al. 1999). Canopy gaps are considered to provide seedlings of many tree species with micro-environmental conditions suitable for their growth (Denslow 1995). Since light is relatively intense in canopy gaps compared with that in the area surrounding gaps, the growth performance of seedlings of most tree species, including pioneer trees that can hardly survive and grow under the forest canopy, is high. Canopy gaps give r-type individuals, which invest little in survivorship or consume resources heavily, a chance to reproduce. Hence gap formation is considered to contribute to the maintenance of tree species diversity and substantially affect the ecological and evolutionary dynamics of many tropical forests (Denslow 1995).

Taking into account that secondary production depends on primary production (Brylinski and Mann 1973; Cole et al. 1988), gap formation is expected to influence organisms that interact with trees. Because areas under canopy gaps have continuously higher resource availability as compared with those under a closed canopy, Levey (1990) categorized canopy gaps as “keystone habitats” for frugivores. However, little is understood about the effects of canopy gaps on the diversity and dynamics of a community of organisms other than the trees. A few studies have evaluated the effects of canopy gaps on fauna or interactions between trees and other organisms, including work on plant–frugivore interactions (Levey 1988, 1990; Beck et al. 2004) and on plant–herbivore interactions (Coley 1983). Thus, the effects of canopy gaps and their role as “keystone habitats” for organisms other than trees have not been adequately studied.

Ants (Hymenoptera: Formicidae) comprise up to 94% of arthropods in insecticidal fogging samples from tropical rain forest canopies and 86% of the biomass of those samples (Tobin 1995; Davidson 1997). Ants often interact with plants both directly over extrafloral nectaries (EFNs) and indirectly over honeydew excreted by myrmecophilous insects such as hemipterans or lepidopteran caterpillars. Ants attend such myrmecophilous insects or EFNs to collect honeydew or nectar, and they protect the myrmecophilous insects or EFN-bearing plants from natural enemies (Hölldobler and Wilson 1990). Thus, ant–hemipteran and ant–plant interactions are sometimes known as mutualisms. Since ants or hemipterans have a close relationship to plants, they would be affected by canopy gaps possessing high plant productivity. However, there is little understanding of the effects of canopy gaps upon ants through their strong relationship with

plants or hemipterans. In this study, we were concerned with the effect of canopy gaps on ant–hemipteran–plant interactions.

Materials and Methods

Study site

The data were collected around the Canopy Biology Plot (8 ha) and the Crane Plot (4 ha) in Lambir Hills National Park, Sarawak, Malaysia (4°2'N, 113°50'E; 50–200 m a.s.l.). The park is located about 10 km inland from the coast in the northern part of Sarawak, and the climate is humid tropical, with a constant high temperature and a weak seasonal change in rainfall (Kato et al. 1995). Most of the park is covered with primary evergreen forests, much of which is classified as lowland mixed dipterocarp forest, thought to be one of the richest forests in the world in terms of the diversity of tree species. The canopy of this multi-layered forest, which has developed on nutrient-poor sandy or clayey soil, is about 35 to 40 m high, with emergent trees penetrating the canopy layer attaining heights of more than 70 m (Kato et al. 1995).

In Lambir Hills National Park, 119 families, 437 genera, and 1153 species of vascular plants were identified by Nagamasu and Momose (1997), and more than 257 ant species have been recorded by Yamane and Nona (1994). Yamane and Nona (1994) also showed that the ant fauna on the ground is different from that on tree trunks (ca. 1 to 1.5 m above the ground).

Ant–hemiptera–plant interactions

There were some open canopy areas in the primary forest, most of which were less than about 100 m² in area. In order to clearly distinguish canopy gaps from closed-canopy areas, we defined canopy gaps as open canopy areas around which we could find a fallen tree. We set up 20 quadrats in canopy gaps at the forest floor (the gap sites); each quadrat was 5 m × 5 m. We also placed a quadrat of the same size about 10 m away from each gap quadrat in a closed-canopy area (the non-gap sites). At each quadrat (a total of 40), all plants taller than 50 cm and with leaves below a height of 2 m above the ground were examined up to a height of 2 m above the ground. We recorded when ants attended EFNs or hemipterans, and collected samples from these plants. All of the collected specimens of ants, plants, and hemipterans (except for a very small number of lost samples) were sorted and identified to species, morphospecies, or higher taxonomic level (genus or family).

We checked the ant-attended parts of the plants for the presence of “shelters” that had been constructed by ants. The ant-attended leaves or shoots were also categorized by color, size, and freshness (hard or soft tissue).

We defined “the frequency of ant–hemiptera interaction” and “the frequency of ant–EFN interaction” as the proportion of plants in which we found ant–hemiptera or ant–EFN interactions (i.e., the number of plants exhibiting such interactions divided by the total number of investigated plants for each quadrat).

We also found some myrmecophytes in the study area. Myrmecophytes prepare special nesting space (domatia) for their obligate ant partners and often provide the ants with food. Most of the obligate mutualisms between ants and myrmecophytes involve scale insects (Hemiptera: Sternorrhyncha: Coccoidea), and ants live only on the plants and feed exclusively on plant food bodies and honeydew excreted by sap-sucking homopterans in the domatia. The ants, in return, protect the plant from herbivores and vines

(Itioka et al. 2000; Fiala and Maschwitz 1990). There is thus a strong relationship between ants, hemipterans, and plants. In this study, we treated the myrmecophytes separately as an independent symbiotic system.

The plants were categorized into three phases of leaf opening, (1) leaves not yet opened, (2) leaves just after opening, (3) plants having both previous categories present. Plants in the third category are defined as having a continuous succession of new leaves available.

Evaluation of light intensity

To assess light intensity, hemispherical photographs were taken with a Nikon camera (Nikon Co., Tokyo, Japan) equipped with an 8-mm fisheye lens at each quadrat. These digital photographs were analyzed using Gap Light Analyzer Version 2.0 (GLA; Frazer et al. 1999). We estimated the amount of direct solar radiation intensity per day ($\text{MJ m}^{-2} \text{d}^{-1}$) at the floor.

Results

Hemipterans and EFN attended by ants

As expected, the frequencies of both ant–hemipteran and ant–EFN interactions were significantly higher at gap sites than at non-gap sites (Wilcoxon signed-rank test, $P = 0.0021$; 0.0026 , respectively). In addition, the species richness of ants, hemipterans, and plants were also higher at canopy gap sites than at non-gap sites. The frequency of myrmecophytes was also higher at gap sites (Wilcoxon signed-rank test, $P = 0.0067$).

Compared with non-gap sites, hemipterans being attended by ants tended to use younger parts of the plants in canopy gaps (Fisher's exact test, $P = 0.017$). Conversely, the proportion of hemipterans around which ants formed a shelter was significantly higher at non-gap sites than at gap sites (Fisher's exact test, $P < 0.001$).

When we classified hemipterans by their movement ability, the groups with relatively good flying ability (e.g., Membracidae and Cicadellidae) tended to appear in gap sites, and other groups with poor flying ability (e.g., Coccoidea and Aphididae) used non-gap sites (Fisher's exact test, $P = 0.016$).

We detected ant–EFN interactions at the young part of plants (e.g., new leaves) (binomial test, $P < 0.001$; young parts = 26, older parts = 4).

Ant–hemipteran–plant interactions

We detected no pattern of specific ants using specific plants or hemipterans, or vice versa. Of 17 ant species found in at least two trophobioses, none was restricted to a single plant family.

Light intensity and new leaf availability of plants

Gap quadrats have a significantly higher ratio of plants with a continuous availability of new leaves compared with non-gap quadrats (Wilcoxon signed-rank test, $P = 0.0018$). Furthermore, this proportion was significantly correlated with the light intensity at the sampling location (Spearman's rank correlation coefficient = 0.41, $R^2 = 0.12$, $P = 0.0093$). The numbers of ant–hemipteran and ant–EFN interactions per quadrat both increased significantly with the number of plants that have a continuous availability of new leaves.

Discussion

The effect of canopy gaps on plants has been emphasized for a long time (Lawton and Putz 1988; Denslow

1995; Hubbell et al. 1999; Galhidy et al. 2006). In this study, we revealed that there is a higher proportion of ant-attended plants in canopy gaps, as well as a higher number of ants species in canopy gaps, compared with in closed-canopy areas. Since numerous arboreal ants in tropical rain forests feed mainly as herbivores or on insect exudates (e.g., from hemipterans; Davidson et al. 2003), canopy gaps may be an important factor in sustaining the biomass and diversity of ants in tropical rain forests. Moreover, plants and hemipterans that offer liquid food to ants were also diverse in canopy gaps. These results indicate that the canopy gap environment influences not only plants but also ant–hemipteran–plant interactions.

In addition, these effects are varied and not limited to certain species or interactions because no patterns of specificity were found. Furthermore, certain ant species used EFNs and hemipterans simultaneously on the same plants. This plasticity will enable ants to use nearby plants both directly and indirectly. It is likely that the complex web containing potential species replacements leads to the maintenance of species diversity in canopy gaps. Plants in canopy gaps act as a food supply not only for ants that live in the gaps but also for those in the surrounding closed-canopy areas because most of the ant species found in the non-gap areas were also found at the canopy gaps. Levey (1990) described canopy gaps as keystone habitats for frugivores because of the availability of abundant food resources. Similarly, we can say that canopy gaps also work as essential space—as Levey put it, “keystone habitats”—for ants and ant–hemipteran–plant interactions.

Judging from our results, we speculate that canopy gaps have a more multifarious influence than previously thought. They may contribute to increasing and maintaining diversity for various groups, especially in the tropical forest. We expect that future studies of insects (besides ants and hemipterans), other arthropods, and mammals and of other ecosystems will demonstrate the great effect of canopy gaps.

Ant-attended hemipterans and EFNs tended to be present on the younger parts of plants. It is likely that the increased amount of sunlight reaching the forest floor in canopy gaps causes the increased number of new leaves and brought about the increase in ant–hemipteran–plant interactions.

The occurrence of canopy gaps is unpredictable, and they do not last long. The fact that hemipterans with relatively good flying ability appeared in canopy gaps shows that the ability to move enables hemipterans to become established on the productive plants in canopy gaps. Conversely, closed-canopy areas are stable compared with canopy gaps. Therefore, hemipterans with limited migration ability found in the shaded understory might put a greater value on a stable relationship with ants rather than on the increased resource availability in gaps. The flight ability of hemipterans may thus represent an adaptation to their preferred environment (i.e., gap vs. non-gap). Our results show that the variations of plants caused by canopy gaps can affect fauna or mutualisms through the process of a nutritional cascade. A slight environmental difference might produce variation in the quantity and quality of interactions. MacArthur et al. (1966) suggested that, because of the higher structural heterogeneity in tropical forests than in the temperate areas, tropical individuals should have higher habitat specificity than individuals in the temperate zone. It was observed in our study that canopy gaps work as keystone habitats for ants and ant–hemipteran–plant interactions, and adaptations to different environments (i.e., gap vs. non-gap) are also important for maintenance of species diversity. Our results should provide insights into the maintenance of species diversity in the tropical rain forest.

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