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Trophobioses on Borneo Climbing Bamboo – diversity and ecology of ant-hemipteran associations on *Dinochloa trichogona* (Poaceae)

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Abstract. Trophobioses between ants and hemipterans play an important role in tropical rainforests. The Borneo Climbing Bamboo *Dinochloa trichogona* commonly occurs in the understorey of lowland forests on Borneo where it frequently hosts trophobioses. Twenty-eight species of ants attending ten species of hemipterans were found on these plants. Coreid bugs and delphacids contributed the majority of associations. On average, 25 % of the stems were infected with trophobioses. Some ants built shelters over their hemipteran partner to protect them. When offered an artificial food resource, the hemipterans were not abandoned completely. *D. trichogona* seems to be a keystone species for ants in the forest understorey, since a large proportion of understorey trophobioses was found on this plant.

Keywords: climbing bamboo, *Dinochloa*, hemiptera, trophobioses, tropical rainforests

INTRODUCTION

For many species of ants living in tropical rainforests, exudates from hemipterans are a crucial source of carbohydrates and amino acids (Davidson 1997). In order to secure these honeydew sources, many ant species care intensively for their hemipteran partner. Such an association is called trophobiosis (Buckley 1987). Ants benefit hemipterans by protecting them against predators and parasitoids and removing the exudates (Way 1963). Some species of *Dolichoderus* herdsman ants even carry hemipterans regularly to new host plants and bring them into their nest (Maschwitz & Hänel 1985, Dill *et al.* 2002).

In South East Asian rainforests, several species of bamboo are common and frequently used by trophobiont tending ants (Schellerich-Kaaden & Maschwitz 1998). Giant bamboo, *Gigantochloa* spp., is not only an important food resource for several ant species; its large hollow stems also provide shelter for ant nests (Kaufmann *et al.* 2001, Schellerich-Kaaden 2001, Dorow 1995, Liefke *et al.* 1998). Some genera of bamboo, like *Gigantochloa*, *Dendrocalamus* and *Schizostachyum*, have extrafloral nectaries under auricles which can be an important sugar resource for ants (Schellerich-Kaaden & Maschwitz 1998). While many studies focus on Giant bamboo, only a few studies mention Climbing bamboo. The Borneo Climbing Bamboo *Dinochloa trichogona* S. Dransf is a common plant in the understorey of mature and secondary rainforests in Borneo (Yap *et al.* 1995, Brühl 2001). This plant is an important host plant for a number of sap-seeking insects (Blüthgen *et al.* 2006). The aims of this study were to show which hemipteran species lived on Climbing bamboo and which species of ants were associated with them.

MATERIAL AND METHODS

This study was carried out in the understorey and tree fall gaps of a mature lowland evergreen dipterocarp forest in the Danum Valley Conservation Area (Sabah, Malaysia). Mean annual rainfall is 2669 mm and mean temperature is 26.7° C (measurement period from 1985 to 1998) (Walsh & Newbery 1999). The investigated area was within a 1.5 km radius around the research station (4°58' N, 117°48'E, 170 m a.s.l.). Initially the vegetation along the forest trail was scanned for Climbing Bamboo (*Dinochloa trichogona*), which was investigated for trophobioses during daytime (09:00 to 16:00h). A trophobiosis was defined as an assemblage of ants and hemipterans on the same plant stem. Some ant species were only found during non-systematic night observations (21:00 to 23:00h) (for details see Blüthgen *et al.* 2006). The same procedure was used to detect an additional 148 trophobioses on 38 species of plants in the forest and on secondary vegetation around the field centre; results are published elsewhere (Blüthgen *et al.* 2006).

From each trophobiosis, a few ants and hemipterans were collected and identified where possible (Carver *et al.* 1991; Bolton, 1994; Dorow, 1995; Dill *et al.* 2002) or at least sorted to morphospecies according to external characters. Some taxa were later identified by taxonomists (see Acknowledgements).

In order to test whether ants leave their hemipteran partners when additional food is offered, a sugar bait experiment was performed.

We used small plastic tubes as bait holders, filled with 20 % (w/v) sucrose solution. This concentration is typical for honeydew (Blüthgen *et al.* 2004). Ants were able to consume the solution via a 3cm-long cotton wick (method used by Lanza *et al.* 1993, Blüthgen *et al.* 2006). Around each trophobiosis, five of these sugar baits were placed. These plastic tubes were attached to the bamboo stem by a plastic tape or stuck through the leaves. Ants were surveyed before installing the baits and after one hour. This experiment was also carried out on 21 trophobioses on other plants too in order to compare the results with bamboo (seven plant species: *Beilschmiedia micrantha* (Lauraceae), *Brownlowia peltata* (Tiliaceae), *Spatholobus* sp. (Fabaceae), *Mallotus floribundus* (Euphorbiaceae), *Parashorea* sp. (Dipterocarpaceae), *Polyalthia* sp. (Annonaceae) and one unidentified climber species). On these plants hemipterans of the Aleyrodidae, Cicadellidae, Membracidae, Pseudococcidae and Psyllidae were found associated with the ants *Crematogaster*, *Dolichoderus*, *Lophomyrmex* and *Technomyrmex*. For a control, ten trophobioses (three on bamboo and seven on other plants) used in this experiment were randomly chosen. Around these trophobioses, plastic tubes filled with water were offered to the ants instead of sugar solution. This control experiment was used to test whether ants leave their hemipterans as a response to disturbances during bait installation or fluid availability. Our study was carried out from July to October 2004.

RESULTS

Associated species

In total, 70 trophobioses on *D. trichogona* were found involving ten species of hemipterans (six families) which were attended by 28 ant species (three subfamilies and nine genera) (Table 1). Of these ants, *Camponotus gigas* (Latreille, 1802) and *Camponotus* sp. (cf. *irritabilis* (Smith,1857)) were found only during night time. A delphacid was the most commonly found hemipteran, in 37 trophobioses, followed by a coreid in 25 associations. The most commonly found ant partners were *Camponotus* sp. (cf. *arrogans* (Smith, 1858)) (15 trophobioses) and *Lophomyrmex bedoti* Emery, 1893 (ten trophobioses). Of the more common hemipterans, coreids were associated with 15 ant species (Fig. 1) and delphacids with 16 ant species. Pupae of Aleyrodidae were visited by nine ant species. The mealybug *Promyrmococcus* sp. (tribe Allomyrmococcini) was always associated with its herdsman partner, *Dolichoderus maschwitzi* Dill, 2002. In five cases, coreids and delphacids were found together in mixed-association trophobioses. In one case, delphacids were found together with the mealybug *Pseudococcus*

Fig. 1. *Crematogaster* (*Paracrema*) *modiglianii* was one of fifteen ant species associated with coreid bugs on *Dinochloa trichogona.*

bambusifolii (Takahashii, 1951). In two cases, two species of ants were found together in one trophobiosis (*Cataulacus* sp. both times, together with *Polyrhachis* sp. 7 and *Paratrechina* sp. 1 respectively). In one case, delphacids were found together with *Promyrmococcus* sp. with both being guarded by the mealybug herdsman partner.

Of 248 bamboo plants checked for infestation in five locations, 26 % were infested by hemipterans (between 10 % and 50 % at the five locations). Of these plants, 10 % were infested by coreids, 12 % by delphacids and 1 % by both hemipterans together. Another 4 % were colonized by other hemipterans (coccids and mealybugs). The coreids, delphacids and coccids were found only on bamboo, while Allomyrmococcini and psyllids were also recorded on other plants. Four of five trophobioses with *Promyrmococcus* sp. and one of two with *Bolbococcus sabahanus* Williams, 2002 were found on bamboo; the others were observed on seedlings of *Parashorea* sp. (Dipterocarpaceae) and on *Etlingera* sp. (Zingiberaceae), respectively. Psyllids were found in eight trophobioses, but only one of them was on *D. trichogona* (all others on *Spatholobus* sp., Fabaceae).

Twenty trophobioses on bamboo were found in the understorey of the mature forest (comprising 31 % of all trophobioses found there) and 45 occurred in tree fall gaps (58 % of all trophobioses surveyed in this habitat). Only five trophobioses were discovered on bamboo in areas covered with secondary vegetation bordering the mature forest.

Life history traits

Four ant species (*Camponotus* (cf. *arrogans*) sp., *Crematogaster modiglianii* (Emery 1900), *Crematogaster* (*Orthocrema*) sp. and *Lophomyrmex bedoti*) built shelters from sand and soil to cover their trophobiotic sites. Thirteen trophobioses with three hemipteran species (coreids, delphacids and unidentified hemipterans) were covered by shelters. Delphacids (11 of 32 trophobioses) were found significantly more often under these shelters than coreids (one of 25 trophobioses) ($Chi^2 = 7.8$; $P < 0.005$). We did not record any ant nests inside shelters or in any parts of the climbing bamboo.

The hemipteran species were found on different parts of the bamboo. Coreids and delphacids were founds on the stems, particularly under small leaves (21 of 26 trophobioses with coreids and 23 of 37 trophobioses with delphacids). In contrast, Allomyrmococcini were always found on the open stem (five trophobioses), while coccids were found on the upper side of the bamboo leaves (nine trophobioses). For both coreids and delphacids, all development stages were found; 21 % of the coreids and 43 % of the delphacids were adults.

Sugar baits were used to distract ants from their trophobiotic hemipterans. A randomly chosen sample of eleven trophobioses involving four

Table 1. Ant species involved in trophobioses with respective hemipteran taxa. Each column is indicating one hemipteran (morpho-)species. Number of interactions shown. Hemipteran taxa with asterisk (*) belong to the higher taxonomic unit in the previous column. Numbers in parentheses (e.g. SKY xx) are the species numbers of Seiki Yamane.

Ant species	Total interactions	Delphacidae	Coreinae	**Notobitus* sp.*	Aleyrodidae	*Planococcus bambusifolii*	*Promyrmococcus* sp.	*Bolbococcus sabanus*	Hemiptera	Psyllidae	Cicadellidae 5a
Dolichoderinae											
Dolichoderus indrapurensis Forel 1912	2	2	-	-	-	-	-	-	-	-	-
Dolichoderus maschwitzi Dill 2002	5	1	-	-	-	-	4[4])	-	-	-	-
Dolichoderus pastoralis Dill 2002	1	-	-	-	-	-	-	1	-	-	-
Dolichoderus thoracicus (Smith 1860)	2	1	-	-	-	-	-	-	-	1	-
Technomyrmex cf. *albipes* (Smith 1861)	4	2	1	-	1[4])	-	-	-	-	-	-
Technomyrmex sp. 3	1	1	-	-	-	-	-	-	-	-	-
Formicinae											
Camponotus (Colobopsis) cf. *saundersi* Emery 1889 (SKY 86)	4	2[2])	1[2])	-	1	-	-	-	-	-	-
Camponotus (Myrmotarsus) cf. *rufifemur* Emery 1900 (SKY 4)	1	-	1	-	-	-	-	-	-	-	-
Camponotus (Tanaemyrmex) cf. *arrogans (*Smith 1858) (SKY 7)	15	7	7[4])	-	1	-	-	-	-	-	-
Camponotus sp. (SKY 95)	1	-	-	-	1	-	-	-	-	-	-
Camponotus (Myrmotarsus) cf. *irritabilis* (Smith 1857) (SKY 5) [3])	5	1	3	1	-	-	-	-	-	-	-
Camponotus gigas (Latreille 1802) [3])	2	-	1	1	-	-	-	-	-	-	-
Paratrechina sp. 4	2	1[2])	-	-	-	1[2])	-	-	-	-	-
Paratrechina sp. 1[1)]	2	1[2])	1[2])	-	-	-	-	-	-	-	-
Paratrechina sp. 2	1	-	1	-	-	-	-	-	-	-	-
Paratrechina sp. 3	1	-	1	-	-	-	-	-	-	-	-
Polyrhachis sp. 7[1)]	1	-	1	-	-	-	-	-	-	-	-
Polyrhachis (Cyrtomyrma) sp.	1	-	-	-	1	-	-	-	-	-	-
Polyrhachis (Myrmhopla) furcata (Smith 1858)	1	-	-	-	-	-	-	-	-	-	1
Polyrhachis (Myrmhopla) mucronata-group	1	-	-	-	1	-	-	-	-	-	-
Polyrhachis s. str. *bihamata*-group	8	3[2])	5[2])[4])	-	-	-	-	-	-	-	-
Polyrhachis s. str. *ypsilon* Emery 1887	2	-	2	-	-	-	-	-	-	-	-

Table 1 continued.

Ant species	Total interactions	Delphacidae	Coreinae	**Notobitus* sp*.	Aleyrodidae	*Planococcus bambusifolii*	*Promyrmococcus* sp.	*Bolbococcus sabanus*	Hemiptera	Psyllidae	Cicadellidae 5a
Myrmicinae											
Cataulacus sp. 1[1)]	3	1	2[2])	-	-	-	-	-	-	-	-
Crematogaster (Orthocrema) sp. 1	6	2[2])	2[2])	-	1[4])	-	-	-	1	-	-
Crematogaster (Paracrema) modiglianii Emery, 1900	3	3	-	-	-	-	-	-	-	-	-
Crematogaster (Paracrema) coriaria Mayr, 1872	2	-	1	-	1[4])	-	-	-	-	-	-
Lophomyrmex bedoti Emery, 1883	10	9[4])	-	-	1[4])	-	-	-	-	-	-
Pheidologeton cf. *pygmaeus* Emery, 1887	1	1	-	-	-	-	-	-	-	-	-

[1]) two ant species at one trophobiosis
[2]) two hemipteran species at the same trophobiosis
[3]) observed on the trophobioses only at night
[4]) species combination used in sugar bait experiment

hemipteran species attended by seven ant species was tested (species combinations used are marked in Table 1). After one hour, the mean percentage of the ant workers remaining at the trophobioses was 43 % (mean number of ants before = 49 ± 71.6; mean number after = 41 ± 72.7). This is a significant decrease (Wilcoxon test; $n = 11$; $Z = 2.93$; $P < 0.003$). The percentage of ants staying at their trophobiosis increased with the total number of hemipterans (Fig. 2): the more hemipterans involved at the trophobiosis, the smaller the percentage of ants leaving (Spearman correlation $r_s = 0.67$; $P < 0.02$). Only one of eleven trophobioses was completely abandoned and all ants were found on the sugar bait. Trophobioses on other plants (nine plant species, data pooled) showed a similar decrease of ants attending hemipteran when sugar baits where offered (Wilcoxon test; $n = 19$; $Z = 3.5$; $P < 0.001$) but there was no correlation between number of hemipterans and percentage of ants leaving (Spearman correlation $r_s = 0.23$; $P = 0.32$). When water-filled control baits were used, there was no significant difference between the number of ants attending the hemipterans before and after bait installation.

DISCUSSION

Most ant species of this study seem to be relatively opportunistic in their choice of trophobiotic partners (Blüthgen *et al*. 2006). *Dolichoderus* herdsman ants were the exception. These ants maintained a close association with their mealybug partners, but were also found in trophobiotic interactions with hemipterans of other families like delphacids (Dill *et al.* 2002). This was probably the case when hemipterans such as delphacids were already present on the host plant before the herdsman ants arrived with their mealybugs.

For hemipterans living on bamboo, the degree of specificity to host plant of the association seems to be higher. Several coreids, especially those of the genus *Notobitus*, are found exclusively on bamboo and other tall grasses (Maschwitz *et al.* 1987). Delphacids are solely reported on monocotyledonous plants (Carver *et al.* 1991). Allomyrmococcini, the mealybug partners of *Dolichoderus herdsman*, are carried by their ant partner to host plants of a very broad taxonomic range including both monocotyledonous and dicotyledonous plants (Dill *et al.* 2002). According to Dill *et al*. (2002), at least four mealybug species of this tribe can be found on several species of bamboo in the genera *Gigantochloa*, *Bambusa* and others. The psyllids are obviously no specialists on bamboo because they were found in larger numbers on other plants, too. It is unlikely that the observed ant species depended on bamboo as a food source, and most species were observed on a broad range of plants (Blüthgen *et al.* 2006). A few ant species during this study were found exclusively on climbing bamboo, but this represented a collecting bias because these ants were rare and found at only one or two trophobioses in total. Much more specialized ant-bamboo associations can be found on larger bamboo like *Gigantochloa* spp. which deliver a nesting resource for ants (Kaufmann *et al.* 2001; Schellerich-Kaaden 2001). At least 80 ant species in South-East Asia use this resource for nesting sites, and some use no other nesting sites (Buschinger *et al.* 1994): ant species like *Polyrhachis arachne* Emery, 1886 and *Polyrhachis hodgsoni* Forel, 1902 build silk pavilions under broad leaves of bamboo where they tend hemipterans (Dorow & Maschwitz 1990). Dorow, (1995) reported that *P. arachne* uses hollow bamboo internodes as nest chambers, while *P. hodgsoni* uses carton-silk pavilions between the leaves of bamboo as nest sites.Both ant species use only hemipterans on bamboo. Several other ants, like *Cataulacus muticus* Emery 1898 (Maschwitz & Moog 2000) or *Polyrhachis schellerichae* Dorow 1996 (Liefke *et al.* 1998), are adapted to build their nest inside the hollow stems of giant bamboo. The latter species keeps hemipterans exclusively inside the bamboo internodes. No incidence was found where ants used *D. trichogona* as a nesting resource.

A trophobiotic relation is questionable for the association of *Pheidologeton* sp. (cf. *pygmaeus* Emery, 1887) and delphacids. Several sugar baits were attended by this species (unpublished data) so it is possible that this species attended delphacids to get their exudates. A further survey

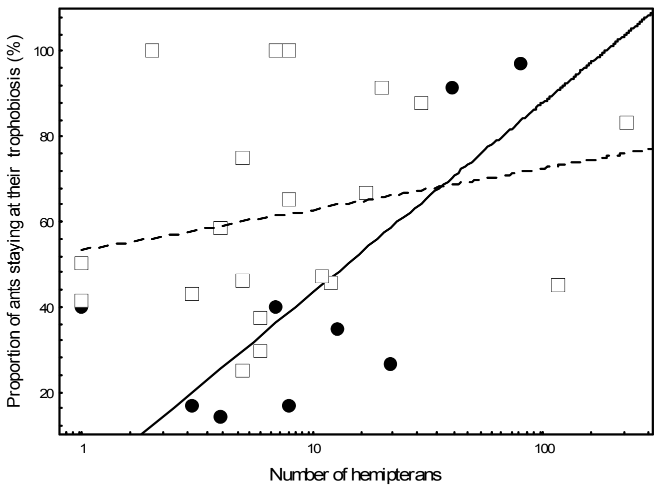

Fig. 2. Ant persistence at their hemipterans, while sugar baits were offered, increases with the size of the trophobiosis (number of hemipterans, log scale). Reobservation of ants was conducted one hour after the presentation of the baits. Trophobioses on *D. trichogona* (●) ; trophobioses on other plants (□) The lines show functions of trophobioses (black line of Climbing Bamboo, dotted line of other plants).

of this association showed that all delphacids had disappeared, so it is possible that they were preyed upon by these ants.

Generally, trophobioses between ants and heteropterans are quite rare, while associations with other hemipterans (Auchenorrhyncha and Stenorrhyncha) are common and include a broad range of taxa (Delabie 2001). Trophobioses between ants and coreids are reported from several cases in the Oriental region (Maschwitz & Klinger 1974, Pfeiffer 1996). In Peninsular Malaysia two different species of coreids (*Cloresmus* sp. and *Notobitus* sp.) were reported on *Gigantochloa scortechinii* Gamble visited by ant species of several genera like *Crematogaster, Camponotus* and the invasive *Anoplolepis gracilipes* (Smith 1857) (Maschwitz *et al.* 1987). Several platispids or shield bugs are associated with ants too; these associations were reported from the Oriental region (Maschwitz *et al.* 1987, Waldkirchner *et al.* 2004) and from the Ethiopian (Giberau & Dejean 2001, Dejean *et al.* 2002). Shield bugs are replaced in the Neotropics by Discocephalinae, a subfamily of the Pentatomidae (Stahel 1954).

The sugar bait experiment showed that the vast majority of trophobioses were not abandoned completely when large resources were offered as an alternative. This suggests hemipterans were considered a valuable and continuous resource of food which was not abandoned for a short-term larger resource. Similar to our results, a study about aphids showed that a smaller percentage of attending ants left a trophobiosis when the association was larger (Katayama & Suzuki 2003).

In addition to honeydew, bamboo may offer other food resources for ants. At least some species of *Gigantochloa, Dendrocalamus* and *Schizostachyum* have sugar excretions on culm sheath auricles (Schellerich-Kaaden & Maschwitz 1998). It is possible that *D. trichogona* possesses similar nectaries because sometimes ants could be observed licking at certain parts of the plant (personal observation). If confirmed this would underline the importance of this plant because it would deliver a further food resource for ants. In coreids and delphacids, all developmental stages were found during the whole time. This suggests a rather stable availability of honeydew for a a relatively long time due to overlapping generations of both insect groups. Some plants have been suggested to play a key role as honeydew sources elsewhere in other ecosystems. For instance, two species of lianas, *Caesalpinia traceyi* (Caesalpianaceae) and *Entada phaseoloides* (Mimosaceae), support the majority of trophobioses of *Oecophylla smaragdina* (Fabricius 1775) in an Australian rain forest (Blüthgen & Fiedler 2002). In some New Zealand beech forests two species of scale insects (*Ultracoelostoma assimile* and *U. brittini*, Margarodidae) living on several species of *Nothofagus* (Nothofagaceae) deliver honeydew resources for a broad range of invertebrates and vertebrates (Beggs & Wardle 2006). It seems that Climbing Bamboo might represent a similar keystone species for ants inhabiting the forest understorey in Bornean rainforests by providing hemipterans which are a sought-after source for honeydew. This plant is very common in the forest understorey, and its hemipteran assemblage is diverse and attracts a very species-rich ant community.

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