

Research article

Ant-hemipteran trophobioses in a Bornean rainforest – diversity, specificity and monopolisation

N. Blüthgen, D. Mezger and K.E. Linsenmair

Department of Animal Ecology and Tropical Biology, Biozentrum, University of Würzburg, Germany,
e-mail: bluethgen@biozentrum.uni-wuerzburg.de, dirk.mezger@gmx.de, ke_lins@biozentrum.uni-wuerzburg.de

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Abstract. Trophobiotic interactions between ants, hemipterans and plants play an important role for all three partners. This study compared a broad spectrum of trophobiotic associations in a tropical rainforest in Sabah, Borneo. We studied partner specificity, ant recruitment, temporal continuity and monopolisation in 218 trophobioses, comprising 58 ant species, 62 hemipteran and over 31 plant species. The most common associations involved *Dinochloa trichogona* (Poaceae) with coreids and delphacids in the forest understorey, and the invasive weed *Chromolaena odorata* (Asteraceae) with *Aphis gossypii* and *A. spiraeola* in the open vegetation; both associations were attended by a broad spectrum of ant species. In general, associations between hemipterans and plants were highly and significantly specialised, while ants were more opportunistic in their choices of partners, although partitioning was also significant between ant versus hemipteran species and consequently between ant versus plant species. The number of ant workers increased significantly, but at a declining rate, with the number of hemipterans at a trophobiosis. Most trophobioses (96%) were only tended by a single ant species at a time and thus effectively monopolised. Occasionally these guards were replaced by another ant species after a few weeks (11%) or during the night (34%). In order to test whether other sugar-seeking ants as potential competitors occurred in the vicinity of trophobioses, sugar baits were placed next to the trophobioses, on a different branch of the same plant, and on a neighbouring plant. While the hemipteran-tending ant colony mostly monopolised the nearest sugar bait, the number of ant species on more distant baits was significantly higher. Our results show that ant associations with honeydew-producing hemipterans may be relatively opportunistic at the community level, but highly predictable on a smaller spatio-temporal scale in respect to recruitment to, and long term securing of this important resource.

Keywords: Formicidae, Hemiptera, mutualism, tritrophic interaction networks, tropical rainforests.

Introduction

Ants are by far the most dominant arthropods in tropical rainforests in terms of biomass and abundance, and they govern key functions in their ecosystems (Beattie, 1985; Hölldobler and Wilson, 1990; Davidson, 1997). Most ants are omnivores (Stradling, 1978). However, it has been predicted that such a large biomass of arboreal ants can only be sustained through a mainly plant-based diet (herbivory), since second-level consumers (predators) are typically rare compared to their prey (Tobin, 1994; Davidson, 1997). Recently, measurements of stable nitrogen isotopes have confirmed this idea and showed that the extent of primary consumption is very high in many arboreal ant species in tropical forests on three continents (Blüthgen et al., 2003; Davidson et al., 2003). Extrafloral and floral nectar, food bodies, fruit flesh and wound exudates may contribute to the ants' primary consumption, but one of the most important resources quantitatively is probably honeydew (Davidson, 1997; Blüthgen et al., 2000b, 2004b; Dejean et al., 2000b). Honeydew is defined as sugary excretions from plant-sucking hemipterans, often representing more or less modified plant sap. It is usually consumed by ants in direct association with the hemipterans (trophobiosis) or indirectly when harvested from excretions accumulated on foliage and other plant surfaces (Way, 1963; Delabie, 2001). Ants may protect hemipterans against predators, parasites and pathogens, and the associated plants against other herbivores, hence the tritrophic association can be often regarded as three-partner mutualism (Buckley, 1987; Cushman and Whitham, 1991; Gullan, 1997; Morales, 2000; Wimp and Whitham, 2001).

Given the importance of honeydew as a resource, it is expected and often observed that nutritious trophobioses are defended by ants against competitors and effectively monopolised (Jackson, 1984; Dejean et al., 1997; Blüthgen et al., 2000b, 2004b; Wimp and Whitham, 2001; Blüthgen and Fiedler, 2004a).

While many detailed studies focus on trophobioses of a focal ant, hemipteran or plant taxon (Del Claro and Oliveira, 1999; Blüthgen and Fiedler, 2002) or on crops (Bigger, 1993), few investigations have been performed on natural communities including a range of species of all three trophic levels (Wood, 1984; Rico Gray, 1993; Rico Gray et al., 1998; Blüthgen et al., 2000b; 2004b, see also Delabie, 2001). Tropical rainforests harbour the highest diversity of plants, ants, and hemipterans, but are particularly understudied. In South-East Asian rainforests, the unique ‘herdsmen ants’ (*Dolichoderus* spp.) have been studied intensively; these maintain a nomadic lifeform with trophobiotic pseudococoids (Maschwitz and Hänel, 1985; Dill et al., 2002). In addition, ant-hemipteran associations in some myrmecophytes (plants bearing ant-inhabited domatia) have been examined in detail (Fiala and Maschwitz, 1990; Maschwitz et al., 1991; Gullan, 1997; Heckroth et al., 1998; Mattes et al., 1998; Moog et al., 2005) as well as interactions involving specific hemipterans or ants (Maschwitz et al., 1987; Klein et al., 1992; Gullan et al., 1993; Schütze and Maschwitz, 1993; Pfeiffer and Linsenmair, 2000; Shingleton and Foster, 2000; Malsch et al., 2001). Several trophobiotic systems involving myrmecophytes, root trophobioses, or herdsmen ants may be relatively specialised due to co-dispersal or vertical transmission of trophobionts by ants (Klein et al., 1992; Malsch et al., 2001; Dill et al., 2002). However, active hemipteran transfer is an exception. It is probably absent in other specialised plant-ants such as *Cladomyrma* (Moog et al., 2005) or *Crematogaster* on *Macaranga* (Brigitte Fiala, pers. comm.), and has not been observed in most other facultative trophobioses. In such cases, pronounced specificity between trophobiotic partners may indicate common habitat or resource requirements, behavioural, morphological or physiological constraints, or competitive exclusion.

The goals of our study were (1) to survey a broad spectrum of non-myrmecophytic above-ground trophobioses in a Bornean rainforest understorey, (2) to examine the degree of partner-specificity between associated plants, hemipterans and ants, (3) to investigate variation in the number of ant individuals per hemipteran across different trophobioses, (4) to study the temporal stability of the associations, and (5) to examine whether trophobioses were commonly monopolised by a single ant colony and whether this monopolisation was based on active competitive exclusion.

Material and methods

The study was carried out in the understorey of a mature lowland evergreen dipterocarp forest in the Danum Valley Conservation Area (Sabah, Malaysia) and adjacent secondary vegetation between July and October 2004. The investigated area was mostly within 2 km radius around the

field centre (4°58' N, 117°48' E, 170 m a.s.l.). Mean annual rainfall is 2669 mm, mean temperature 26.7°C (Walsh and Newbery, 1999). Initially we surveyed the entire vegetation along paths for trophobioses; later our survey was biased towards the most common host plants. The unit of our survey of trophobioses and count of trophobionts was the individual plant. All ant-tended hemipterans on an individual plant (nymphs over ca 1 mm body length and adults) and all ant workers close to the hemipterans were counted *in situ* as a ‘snapshot’ (usually within 1–3 min) during daytime (09:00–16:00 h). For some trophobioses, counts were repeated on average 10 days (range 2–50) and again 32 (21–66) days after the first survey (for 75% versus 42% of all trophobioses, respectively), and/or during nighttime within 7 (0–23) days (20:00–22:00 h, 28%). From a total of 218 trophobioses investigated, 35% were located in open secondary vegetation, 35% in gaps within the mature forest, and 29% in the understorey of the mature forest. Ant and hemipteran specimens were collected from all locations, sorted and identified by one of us (D. Mezger) where descriptions of characters were available for species or higher taxa (Ettershank, 1966; Carver et al., 1991; Bolton, 1994; Dorow, 1995; Eguchi, 2001; Dill et al., 2002), or at least assigned to morphospecies based on external morphological characters, some of which were later confirmed or identified by taxonomists (see Acknowledgements). Note that the morphospecies assignment of hemipterans is problematic where only nymphs could be collected (several cicadellids and membracids); we thus present data for both a maximum and a conservative number of morphospecies. Collection of specimen was performed following observations and counting to minimise disturbance. Usually only one or very few ants and hemipterans were removed, and repeated surveys only included associations where several hemipterans remained after collection.

Species partitioning between hemipteran-plant, hemipteran-ant and plant-ant associations was analysed using a $r \times c$ randomisation algorithm described in Blüthgen et al. (2000a). The two-dimensional entropy across the matrix, $H = -\sum_i \sum_j (p_{ij} \log p_{ij})$, was calculated based on the observed association matrix (e.g. ant species \times hemipteran species). In this matrix, each cell entry p_{ij} represents the proportion of interactions between species i and species j of the total number of interactions observed (e.g. the interaction frequency of a certain ant species i with a certain hemipteran species j divided by the total number of interactions). We compared H of the observed matrix with the distribution of the statistic of randomly generated matrices (H_{ran}) of fixed row and column totals (10^5 randomisations performed). The strength of species partitioning was calculated as $H' = (H - H_{min}) / (H_{max} - H_{min})$, where H_{max} and H_{min} are the largest and smallest possible entropy, respectively, for matrices with the same row and column totals. Hence, H' ranges between zero (for a random distribution) and one (for the maximum degree of partitioning). In order to avoid pseudoreplication in the analysis of species partitioning, replicate associations between species within a putative single ant colony (within ca 50 m radius) were removed from the data set.

An ant bait experiment was carried out to investigate whether additional sugar-feeding ants occurred in the vicinity of trophobioses and were possibly excluded by the trophobiont-tending ant colony. We compared the number of ant individuals and species on sugar baits placed (a) next to the trophobiosis, (b) on a different branch of the same plant, but in greatest possible distance from the trophobioses, and (c) on a neighbouring plant. As baits we used standard microcaps (2 ml) filled with 20% (w/v) sucrose solution (typical concentration for honeydew, see Blüthgen et al., 2004a). The solution was available to ants through a 3 cm long cotton wick (method used by Lanza et al., 1993; Blüthgen and Fiedler, 2004b). One bait each was attached to twigs or leaves at the three places (a–c) around a trophobiosis, and replicated for 60 independent trophobioses attended by 23 ant species (marked in Table 1). Ants were surveyed 1 h and 24 h after bait installation. For each bait, the number of ant individuals and species from both surveys were pooled; data from baits with no ants were excluded from analyses.

All data involving counts of ants (a) and hemipterans (h), or their ratio (alh) were normalised via log transformation prior to ANOVA or regression analyses. The average alh ratio (i.e. the slope of the regression of a over h) for n measurements was back-transformed as $\exp[n^{-1}(\log a / \log h)]$.

Table 1. Ant species involved in trophobioses with respective hemipteran taxa. Number of spatially separated interactions shown (independent colonies). Several uncommon ant species (each $n \leq 3$) pooled to genera. Hemipteran taxa with asterisk (*) belong to the larger taxonomic unit in the previous column.

Hemiptera															
Ant species (subfamily)	Notes ¹⁾	Total (interactions)	Membracidae (13 spp. ⁶⁾	Cicadellidae (22 spp. ^{6) 7)}	Delphacidae (1 sp.) ⁷⁾	Aleyrodidae (1 sp.) ⁷⁾	Aphidae (1 sp.) ⁷⁾	* <i>Aphis gossypii</i> or <i>spiraecola</i> ⁸⁾	Coccidea (9 spp.) ⁷⁾	Margarodidae (<i>sensu lato</i>) ⁷⁾	Pseudococcidae (4 spp.) ⁹⁾	*Allomyrmococcini (3 spp.) ^{7) 10)}	Psyllidae (1 sp.) ⁷⁾	Coreidae (2 spp.) ⁷⁾	Plataspidae (1 sp.) ⁷⁾
Total (interactions)		221	20	51	31	1	1	36	29	1	8	10	8	24	1
Dolichoderinae															
<i>Dolichoderus cuspidatus</i> ^{3) 4)}		1	–	–	–	–	–	–	–	–	–	1	–	–	–
<i>Dolichoderus indrapurensis</i> ⁴⁾	dn	8	2	2	3	–	–	–	1	–	–	–	–	–	–
<i>Dolichoderus maschwitzii</i> ^{3) 4)}	dn	8	–	1	–	–	–	–	–	–	–	6	1	–	–
<i>Dolichoderus pastoralis</i> ^{3) 4)}		2	–	–	–	–	–	–	–	–	–	2	–	–	–
<i>Dolichoderus thoracicus</i> ⁴⁾	dn	22	3	4	1	–	–	5	2	–	3	–	4	–	–
<i>Dolichoderus</i> sp.2		1	–	–	–	–	–	1	–	–	–	–	–	–	–
<i>Technomyrmex</i> cf. <i>albipes</i> ^{4) 5)}	dn	10	1	3	2	–	–	2	1	–	–	–	–	1	–
<i>Technomyrmex</i> (3 spp.) ^{4) 5)}	dn	3	–	–	1	–	–	–	2	–	–	–	–	–	–
Formicinae															
<i>Anoplolepis gracilipes</i>		4	–	–	–	–	–	3	1	–	–	–	–	–	–
<i>Camponotus</i> cf. <i>arrogans</i> ^{4) 5)}	dn #4	16	–	3	5	–	–	–	3	–	–	–	–	5	–
<i>Camponotus gigas</i>	n	3	–	1	–	–	–	–	–	–	–	–	–	2	–
<i>Camponotus</i> cf. <i>irritabilis</i>	n #5	5	1	1	1	–	–	–	–	–	1	–	–	1	–
<i>Camponotus reticulatus</i>	#6–#7	2	–	–	–	–	–	2	–	–	–	–	–	–	–
<i>Camponotus rufifemur</i>	dn #1–#3	2	–	–	–	–	–	–	–	–	–	–	1	1	–
<i>Camponotus</i> cf. <i>saundersi</i>	dn	5	–	2	1	–	–	–	1	–	–	–	–	1	–
<i>Camponotus</i> (<i>Tanamymex</i>) sp.1 ⁴⁾	dn #6	4	–	–	–	–	–	3	–	–	1	–	–	–	–
<i>Camponotus</i> cf. <i>dolichoderoides</i> ^{4) 5)}		1	–	–	–	–	–	–	1	–	–	–	–	–	–
<i>Camponotus</i> sp.2	d	1	–	–	–	–	–	–	1	–	–	–	–	–	–
<i>Paratrechina</i> sp.1 ⁵⁾	#8	7	2	3	1	–	–	–	–	–	–	–	–	1	–
<i>Paratrechina</i> sp.3 ⁴⁾	dn #7	3	–	–	–	–	–	1	–	–	1	–	–	1	–
<i>Paratrechina</i> (3 spp.) ⁵⁾	d	6	–	–	1	–	–	3	–	–	1	–	–	1	–
<i>Polyrhachis olybrius</i> ⁴⁾	d	8	1	–	2	–	–	1	–	–	–	1	–	3	–
<i>Polyrhachis ypsilon</i> ⁴⁾	d	3	1	1	–	–	–	–	–	–	–	–	–	1	–
<i>Polyrhachis</i> (7 spp.) ⁴⁾	d #9	7	–	1	1	–	–	2	2	–	–	–	–	1	–
<i>Plagiolepis</i> sp.1		1	–	–	–	–	–	1	–	–	–	–	–	–	–
Myrmicinae															
<i>Cataulacus</i> sp.1	#8–#9	2	–	–	1	–	–	–	–	–	–	–	–	1	–
<i>Crematogaster coriaria</i>	d	2	–	–	–	–	–	–	1	–	–	–	–	1	–
<i>Crematogaster modiglianii</i> ^{4) 5)}	dn #1–#5	33	4	14	5	1	–	–	6	1	–	–	2	–	–
<i>Crematogaster rogenhoferi</i>		2	1	–	–	–	1	–	–	–	–	–	–	–	–
<i>Crematogaster</i> (<i>Orthocrema</i>) sp.1 ⁵⁾	dn	8	–	1	2	–	–	1	2	–	–	–	–	2	–
<i>Crematogaster</i> (<i>Orthocrema</i>) sp.2 ⁵⁾		2	–	–	–	–	–	–	2	–	–	–	–	–	–
<i>Crematogaster</i> (<i>Paracrema</i>) (2 spp.)	dn	3	–	2	–	–	–	–	–	–	1	–	–	–	–
<i>Lophomyrmex</i> cf. <i>bedoti</i> ^{4) 5)}	dn	13	1	6	3	–	–	1	1	–	–	–	–	1	–
<i>Monomorium</i> (2 spp.) ^{4) 5)}	dn	4	–	1	–	–	–	2	1	–	–	–	–	–	–
<i>Myrmicaria</i> (2 spp.) ^{4) 5)}	dn	2	1	–	–	–	–	–	–	–	–	–	–	–	1
<i>Paratopula</i> sp.1	dn	2	–	1	–	–	–	1	–	–	–	–	–	–	–
<i>Pheidole huberi</i>	dn	2	–	1	–	–	–	–	1	–	–	–	–	–	–
<i>Pheidole</i> (2 spp.) ⁴⁾		3	–	2	–	–	–	1	–	–	–	–	–	–	–
<i>Pheidologeton</i> sp.1		1	–	–	1	–	–	–	–	–	–	–	–	–	–
<i>Rhoptromyrmex</i> sp.1		1	–	1	–	–	–	–	–	–	–	–	–	–	–
<i>Solenopsis</i> sp.1		1	–	–	–	–	–	–	1	–	–	–	–	–	–
<i>Tetramorium</i> sp.1	dn	5	1	–	–	–	–	4	–	–	–	–	–	–	–
<i>Tetramorium</i> (2 spp.)		2	1	–	–	–	–	1	–	–	–	–	–	–	–

Table 1. (continued):

- ¹⁾ Diel ant activity at trophobioses checked at night: d – diurnal, n – nocturnal, dn – both (continuously) (all others not checked at night; notes for pooled species apply to one species). Simultaneous honeydew use by two ant species at the same trophobiosis in nine trophobioses (#1–#9), twice in #1
- ³⁾ Herdsman species (Dill et al. 2002)
- ⁴⁾ Ant species involved in sugar bait experiment
- ⁵⁾ Ant species building shelters around some trophobioses using soil or plant substrate
- ⁶⁾ Conservative sorting: 10 Membracidae and 15 Cicadellidae species
- ⁷⁾ Most trophobioses (>85%) in gaps or understorey of mature forest
- ⁸⁾ All trophobioses in open secondary vegetation (neither ⁷⁾ nor ⁸⁾: common in both habitats)
- ⁹⁾ Including *Paracoccus interceptus* and *Planococcus bambusifolii*
- ¹⁰⁾ *Dicranococcus sabahensis*, *Bolbococcus sabahanus*, *Promyrmococcus* sp.

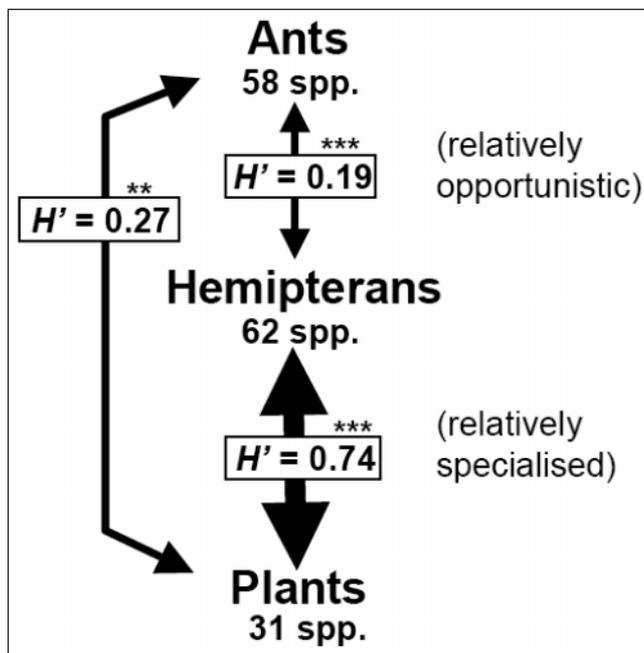


Fig. 1. Species partitioning among partners in tritrophic interactions. Strength of species partitioning (standardized entropy H' , arrow width proportional) shown with asterisks indicating significance level of $r \times c$ randomisation test. Entropy of the observed association matrix (H) and mean \pm SD of randomised associations (H_{ran}) between ants and plants: $H = 4.47$, $H_{\text{ran}} = 4.58 \pm 0.04$, $p = 0.003$; ants and hemipterans: $H = 4.90$, $H_{\text{ran}} = 5.07 \pm 0.03$, $p < 10^{-5}$; hemipterans and plants: $H = 3.85$, $H_{\text{ran}} = 4.51 \pm 0.04$, $p < 10^{-5}$.

Results

Associated species

In total, 218 trophobioses were observed (Table 1), comprising 58 ant species (18 genera). These ants were associated with 62 hemipteran species (11 families; total number of species for conservative sorting of membracid and cicadellid nymphs: 53, see Table 1) on at least 31 host plant species (19 families) (Table 2). Several hemipteran taxa were mainly found in the mature forest and only poorly represented in the open secondary vegetation, except membracids and pseudococcids that were common in both habitats, and two non-native aphids (*Aphis gossypii* and *A. spiraeola*) that were exclu-

sively found in secondary vegetation (Table 1). Most common trophobioses in the forest understorey involved the common climbing bamboo *Dinochloa trichogona* with coreids and delphacids that were exclusively found on this plant and were attended by various ant species. About 26% of the individual *D. trichogona* shoots examined in five locations harboured these trophobioses. In the open secondary vegetation, the invasive weed *Chromolaena odorata* was the most common host of trophobioses. The two aphids (*A. gossypii* and *A. spiraeola*) produced leaf pseudogalls (see Carver et al., 2003) on these plants in which they were attended by a broad spectrum of ant species. These two similar aphid species sometimes occurred in mixed associations and were not distinguished in the following association analyses. They infested 82% of all *C. odorata* individuals checked in five locations.

Mixed associations of hemipteran species from different families occurred in 20 trophobioses (9%). Most common co-occurrences were between the above *Aphis* spp. and pseudococcids on *C. odorata* (5 cases) and delphacids and coreid bugs on *D. trichogona* (5 cases).

Degree of specificity

Associations between species were significantly different from random in all three combinations of trophobiotic partners (Fig. 1), where the specificity of ant-plant associations for these non-myrmecophytic plants is most likely a consequence of ant-hemipteran partitioning. Species partitioning was very strong between plants and hemipterans and much weaker between ants and hemipterans with respect to partitioning strength H' (Fig. 1). H' values based on conservative sorting of hemipteran species (53 spp.) were somewhat lower for plant-hemipteran interactions ($H' = 0.66$), but remained unchanged for ant-hemipteran interactions. Results for species partitioning between plants and hemipterans increased strongly ($H' = 0.86$) when replicates on different plant individuals within a 50m radius were considered (numbers in parentheses in Table 2). Only for the host plant choice of hemipterans may true specialisation be common, while ants, except for *Dolichoderus* 'herdsman' ants, were usually more opportunistic in their choices of associated partners. Within this study the degree of putative 'specificity' (locally restricted and based on sampling method) can be estimated for those species that were observed in at least two trophobioses. Of 13 hemipteran species that occurred in at

Table 2. Plant species hosting ant-tended hemipterans. For species number and remarks on hemipteran taxa, see Tab. 1. Interactions were defined as number of replicates that were separated by more than 50m (total number of plant individuals in parentheses if deviating from the former).

Plant family and species	Plant life-form ¹⁾	Total (interactions) (234) ²⁾	Hemiptera												
			Membracidae	Cicadellidae	Delphacidae	Aleyrodidae	Aphidae	* <i>Aphis gossypii</i> or <i>spiraeola</i>	Coccidae	Margarodidae (<i>sensu lato</i>)	Pseudococcidae ³⁾	*Allomyrmococcini	Psyllidae	Coreidae	Plataspidae
Total (interactions)		126 (234) ²⁾	18	39 (40)	11 (35)	2	1	17 (60)	16 (21)	1	5 (9)	11	7 (9)	13 (26)	1
Annonaceae: <i>Fissistigma</i> sp.	s	2	–	1	–	–	–	–	–	–	1	–	–	–	–
<i>Polyalthia</i> sp.	s	1	–	–	–	1	–	–	–	–	–	–	–	–	–
Asteraceae: <i>Chromolaena odorata</i>	h	19 (66)	1	1	–	–	–	13 (56)	2	–	2 (6)	–	–	–	–
<i>Micania micrantha</i>	c	1	–	–	–	–	–	1	–	–	–	–	–	–	–
Convolvulaceae: <i>Merremia peltata</i>	c	2	1	–	–	–	–	1	–	–	–	–	–	–	–
Costaceae: <i>Costus globosus</i>	h	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Dipterocarpaceae: <i>Parashorea malaanonan</i> or <i>P. tomentella</i>	t	13 (14)	–	11 (12)	–	–	–	–	–	1	–	1	–	–	–
Euphorbiaceae: <i>Mallotus floribundus</i>	s	2	–	1	–	–	–	–	1	–	–	–	–	–	–
<i>Mallotus miquelianus</i>	s	1	–	1	–	–	–	–	–	–	–	–	–	–	–
<i>Mallotus wrayi</i>	s	1	–	–	–	1	–	–	–	–	–	–	–	–	–
<i>Mallotus</i> sp.	s	1	–	–	–	–	–	–	1	–	–	–	–	–	–
Fabaceae: <i>Bauhinia</i> sp.	c	1	–	1	–	–	–	–	–	–	–	–	–	–	–
<i>Caesalpinia</i> sp.	c	1	1	–	–	–	–	–	–	–	–	–	–	–	–
<i>Spatholobus</i> sp.	c	19 (21)	9	4	–	–	–	–	–	–	–	–	6 (8)	–	–
Gen. indet.	c	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Lauraceae: <i>Beischmiedia micrantha</i>	t	2	–	1	–	–	–	–	1	–	–	–	–	–	–
<i>Litsea</i> sp.	s	1	–	–	–	–	–	–	1	–	–	–	–	–	–
<i>Nothaphoebe</i> sp.	s	1	–	–	–	–	–	–	1	–	–	–	–	–	–
Leeaceae: <i>Leea</i> cf. <i>indica</i>	s	5	1	4	–	–	–	–	–	–	–	–	–	–	–
Melastomataceae: <i>Melastoma melabathricum</i>	s	3	1	1	–	–	–	1	–	–	–	–	–	–	–
Meliaceae: <i>Aglaiia</i> sp.	t	3	1	1	–	–	–	–	1	–	–	–	–	–	–
Myrsinaceae: <i>Ardisia</i> sp.	s	1	–	–	–	–	–	–	1	–	–	–	–	–	–
Poaceae: <i>Dinochloa trichogona</i>	c	35 (79)	–	1	11 (35)	–	–	–	4 (9)	–	1	4 (6)	1	13 (26)	–
Rubiaceae: <i>Pleurocarpidia sandanica</i>	h	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Gen. indet.	c	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Tiliaceae: <i>Brownlowia peltata</i>	t	2	–	2	–	–	–	–	–	–	–	–	–	–	–
<i>Pentace adenophora</i>	t	1	1	–	–	–	–	–	–	–	–	–	–	–	–
Urticaceae: <i>Dendrocnide</i> sp.	s	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Verbenaceae: <i>Callicarpa longifolia</i>	s	1	–	–	–	–	1	–	–	–	–	–	–	–	–
Vitaceae: <i>Tetrastigma</i> sp.	c	1	–	1	–	–	–	–	–	–	–	–	–	–	–
Zingiberaceae: <i>Etilingera</i> sp.	h	1	–	–	–	–	–	–	–	–	1	–	–	–	–
Fam. indet.	(all)	14	2	3	–	–	–	1	3	–	1	3	–	–	1

¹⁾ Plant life-forms: c – climber, h – herb, s – small tree or shrub, t – tree

²⁾ Numbers of interactions differ from Tab. 1 where different ant or hemipteran species attended the same plant or area, or where different ants attended the same hemipteran association.

least three trophobioses, four were restricted to a single plant species each (a coreid, a delphacid and a coccid species on *Dinochloa trichogona* and a cicadellid on *Parashorea*), but none of the species occurred with a single ant species only. Of 27 ant species found in at least three trophobioses, none was restricted to a single hemipteran species.

Ant visitation rate

The number of ants (a) visiting a trophobiosis increased significantly with the number of hemipterans (h) (Spearman's $r_s = 0.45$, $p < 0.0001$, $n = 215$ trophobioses) (Fig. 2). This positive correlation was found within the trophobioses

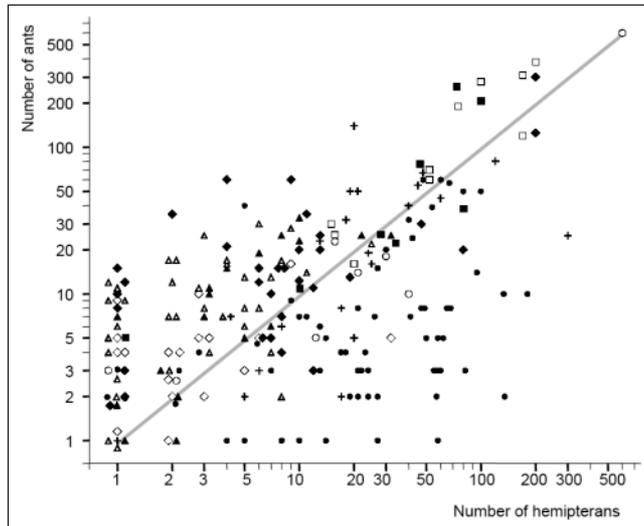


Fig. 2. Number of ants at trophobioses in relation to the number of hemipterans (total 215 trophobioses, log-log scale). The grey line shows a linear function as $f(x) = 0.96x$. Hemipterans: Aphidae (●), Cicadellidae (△), Coccidea (●), Coreidae (★), Delphacidae (+), Membracidae (▲), Pseudococcidae: Allomyrmococcini (□), Psyllidae (■), or other hemipterans pooled (*).

of all hemipteran taxa (groups as in Fig. 2, *a priori* excluding the heterogeneous ‘other hemipterans’; all $r_s \geq 0.43$, $p < 0.01$) except coreid bugs ($r_s = 0.32$, $p = 0.19$). The mean number of ants per individual hemipteran (a/h) was 0.96. Overall, a/h ratios decreased significantly as h increased ($r_s = -0.61$, $p < 0.0001$, $n = 215$ trophobioses). Consequently, residuals from the linear function shown in Figure 2 (slope 0.96 and fitted through zero) are mostly negative for larger trophobioses (large h). This linear decrease of a/h ratio with increasing h occurred within aphids, cicadellids, coreids, and delphacids (all $r_s \leq -0.50$, $p < 0.01$), but not within coccids, membracids, pseudococcids, or psyllids (all $r_s \geq -0.17$, $p > 0.69$). Independently from h , mean a/h ratios differed significantly among hemipteran taxa (ANCOVA: $F_{7,198} = 18.3$, $p < 0.0001$; log h as covariate, groups as in Figure 2 excluding the pooled ‘other hemipterans’). This effect is mostly due to aphid trophobioses (mostly involving *Aphis gossypii* and *A. spiraeola* on *Chromolaena odorata*) that were significantly less attractive in terms of per-capita visitation than all other taxa (Tukey’s HSD, all $p \leq 0.002$). In addition, cicadellids and delphacids received a higher visitation rate than coccids ($p \leq 0.03$). Therefore, residuals from the linear function in Figure 2 were negative for most trophobioses involving aphids and particularly high for cicadellids and delphacids.

Temporal persistence

The majority of ant species attended their trophobioses continuously day and night (Table 1). Only at three small tro-

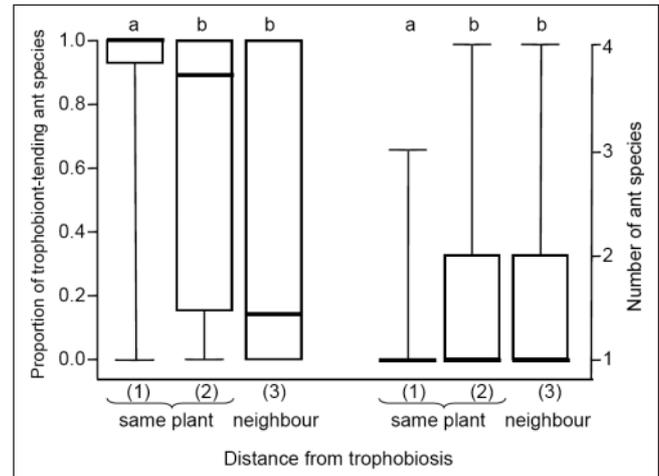


Fig. 3. Ants on sugar baits with increasing distance to trophobioses. Proportion of workers from the trophobiont-tending ant colony and number of ant species during two surveys shown for baits placed (1) next to the trophobiosis, (2) on a different branch of the same plant, and (3) on a neighbouring plant. Boxplots show median, quartiles and range. Different letters indicate significant differences according to pairwise comparisons (Wilcoxon matched pairs, Bonferroni corrected) following Friedman ANOVA (proportion: $\chi^2 = 11.7$, $p = 0.003$; species richness: $\chi^2 = 7.8$, $p = 0.02$).

phobioses (5% of 56 where hemipterans were still present), no tending ants were found during the nocturnal survey. At 19 trophobioses (34%), formerly diurnal ant guards were replaced at night. Fifteen of these cases involved largely nocturnal *Camponotus* species (mostly *C. gigas*, *C. cf. irritabilis*, *C. cf. arrogans*) that replaced *Crematogaster*, *Lophomyrmex*, *Polyrhachis*, *Paratrechina*, or other *Camponotus* species, including four cases where *Crematogaster modiglianii* was replaced by its parabioc partner (*C. cf. irritabilis* or *C. cf. arrogans*).

In many trophobioses that were re-examined at daytime about 10 or 32 days after the first survey, hemipterans were still present during the second survey (63%) or third survey (46%), including eight cases where different hemipteran species were found on the same plant instead. Ant guards of maintained trophobioses were often from the same species as during the first survey, particularly in larger trophobioses. During the second survey, this was true for 81% of the trophobioses, while a change of ant guards occurred in 11%, and hemipterans were at least temporally unattended in 8% of the cases (total $n = 105$). In most cases species-specific relations even persisted until the third survey (77%, 11% changed, total $n = 43$). Trophobioses that were maintained by conspecific ant guards between first and second survey were significantly larger (mean \pm se number of ants 38 ± 10) than those that were abandoned by ants, hemipterans, or both (11 ± 2 ; Tukey’s HSD, $p < 0.001$). Trophobioses with a change of guards had an intermediate size (13 ± 4) and did not differ significantly from the above groups ($p \geq 0.51$; overall effect: ANOVA, $F_{2,161} = 9.1$, $p < 0.001$).

Monopolisation

Most trophobioses were only attended by a single ant species at a time. Only during ten occasions (2.3%) of a total of nine trophobioses (4.1%) were two ant species found together at the same aggregation sampling honeydew. Most of these cases involved *Crematogaster modiglianii* that was found together with *Camponotus* species (Table 1); at least *Camponotus rufifemur* lived in parabioc associations with *C. modiglianii* sharing nests in tree trunks.

Sugar baits next to a trophobiosis were mostly monopolised by the same hemipteran-tending ant colony only (in 72% of 60 trophobioses examined). The average proportion of workers from the trophobiont-tending ant colony in relation to all ants at a bait declined with increasing distance to trophobioses. This pattern was associated with an increase of species richness of baited ants farther away from trophobioses (Fig. 3). Ants other than the trophobiont-tending colony already contributed significantly higher proportions and a higher species richness on different branches of the same plant harbouring the trophobioses, reaching a similar level as ants baited on neighbouring plants (post hoc analysis in Fig. 3). However, some ants that guarded their trophobioses dominated the entire plant and its surroundings more than others. Among the common ant species in the bait experiment, *Dolichoderus thoracicus* and *Crematogaster modiglianii* were the most dominant ones. The former monopolised all three baits including the neighbouring plant in six of a total of 11 trophobioses and two baits in three cases, the latter monopolised all three baits in four cases and two baits in two cases of a total of seven trophobioses. *Camponotus cf. arrogans* and *Lophomyrmex cf. bedoti* also monopolised all baits (1 vs. 3 cases) or two baits (4 vs. 3 cases) of a total of 8 vs. 9 cases, respectively. All other ant species were uncommon in this experiment ($n < 3$) and either monopolised only a single bait or none, except *Myrmecaria* that monopolised both baits on the plant on which its trophobiosis occurred ($n = 1$). Among all ants that were observed at any of the three baits but not at the respective trophobiosis, *Polyrhachis* and *Camponotus* (various species of each) were the most common genera (25% and 14%, respectively, of a total of 80 occurrences). In contrast, *Dolichoderus* (3%) and *Lophomyrmex* (4%) were only rarely, and *Myrmecaria* never involved (the former two mostly at the bait on the neighbouring plant only). Hence, ant species that typically monopolised their trophobioses plus surrounding sugar baits, were only rarely found on sugar baits near trophobioses of other ants.

Discussion

Our survey of largely unspecific trophobioses in a Bornean rainforest revealed a broader spectrum of associated ant, hemipteran and plant species than found in similar investigations in other regions (Rico Gray, 1993; Rico Gray et al., 1998; Blüthgen et al., 2000b; 2004b). Associations between ants and coreid bugs are particularly noteworthy, because

only few cases have been documented between ants and Heteroptera so far (Maschwitz et al., 1987; Dejean et al., 2000a). As in many associations involving 'homopterans' (Way, 1963; Buckley, 1987), ants can actively protect bugs against parasitoids (Gibernau and Dejean, 2001).

On all levels of tritrophic interactions, a highly significant non-random association was found. However, ants were relatively opportunistic in their choices of partner species, while associations between hemipterans and their host plant species were much more specific. Thus, a broad range of ant species may potentially attend a specific hemipteran species. Similarly, an opportunistic use of hemipterans by a number of ant species was found for soldier aphids (Schütze and Maschwitz, 1993; Shingleton and Foster, 2000) as well as in many other tropical systems focusing on a certain hemipteran taxon (e.g., Wood, 1984; Del Claro and Oliveira, 2000). In contrast, species partitioning between ants and hemipterans was much more pronounced in a species-poorer Australian rainforest community (Blüthgen et al., 2004b; their association matrix yields $H' = 0.52$). Moreover, in more protected systems such as associations in myrmecophytes or other ant nest cavities, a higher degree of specialisation between ants and hemipteran partners is expected, often involving mutual adaptations of both partners (Fiala and Maschwitz, 1990; Maschwitz et al., 1991; Klein et al., 1992; Gullan et al., 1993; Gaume et al., 1998; Heckroth et al., 1998; Mattes et al., 1998; Moog et al., 2005). The same specificity is expected for more obligate systems where ants largely depend on honeydew, mostly pronounced in *Dolichoderus* herdsman ants (Maschwitz and Hänel, 1985; Dill et al., 2002). However, comparisons across all of these studies are problematic, since partner-specificity has been poorly quantified so far.

Most trophobioses were effectively monopolised by an ant colony on a small spatial scale, as commonly observed elsewhere (Jackson, 1984; Dejean et al., 1997; Blüthgen et al., 2000b, 2004b; Wimp and Whitham, 2001). Few trophobioses in our study deviated from this rule, most notably parabioc *Crematogaster modiglianii* – *Camponotus* spp. associations or small trophobioses involving few ant and hemipteran individuals (see also Dejean et al., 2000a; Delabie, 2001). Monopolisation of trophobioses by ants often persisted over time. Moreover, changes of ant guards between day and night or over the course of weeks were relatively limited, and especially rare for larger trophobioses. Discontinuities in ant attendance and diurnal turnover may vary across species and habitats (Dejean et al., 2000a,c; Del Claro and Oliveira, 2000; Delabie, 2001). The facultative construction of pavillons around trophobioses, as seen in several ant genera (see also Way, 1963; Dumpert et al., 1989; Blüthgen et al., 2000b; Gibernau and Dejean, 2001; Weißflog, 2001; Blüthgen and Fiedler, 2002), may function to defend and monopolise their honeydew sources.

Other sugar-seeking ants often foraged on the same plant, but almost never visited the trophobiosis, and they were very rarely found on sugar baits in close proximity to the trophobiosis. The monopolisation of a trophobiosis most likely results from an active territorial defence by the tending ant col-

ony. Our sugar bait experiments give a strong indication of such competitive exclusion. In the absence of competition, all baits should have a similar probability of being detected and attended. However, species richness of ants other than the trophobiont-tending colony strongly increased with distance to a trophobiosis. Moreover, ant species that utilised these baits in addition to the ant that guarded its trophobiosis, were most often relatively subordinate species (e.g. several *Polyrhachis* and *Camponotus* spp.) rather than dominant, aggressive ones (*Dolichoderus*, *Crematogaster*) with large colonies that tend large trophobioses elsewhere (see e.g. Majer, 1993; Davidson, 1997; Dejean and Corbara, 2003 for congeneric species and their dominance status). This asymmetry supports the concept of ‘ant mosaics’, which states that dominant ant colonies defend mutually exclusive territories, but co-occur with a spectrum of subdominant or subordinate species (Les-ton, 1973; Jackson, 1984; Majer, 1993; Dejean et al., 1997; Wimp and Whitham, 2001; Dejean and Corbara, 2003; Blüthgen et al., 2004b). Since most ant species that may become superdominant in terms of abundance and competition hierarchies seem to be highly dependent on trophobionts (Davidson, 1997), mutual exclusion among such dominant ants may result from interspecific competition for honeydew sources. Subordinate species may be less likely to imperil a dominant ant’s trophobiosis and could be tolerated to some degree in the proximity of a trophobiosis without interference. Resource monopolisation may be often limited to a small scale, e.g. the immediate surrounding of a trophobiosis, although some highly dominant hemipteran-tending ants such as *Dolichoderus thoracicus* were found to extend their negative impact on the activity of other ants across the entire plant or adjacent area in this study. Overall, the distribution of productive trophobioses or other sustainable resources may be a key factor for the distribution and community composition of ants and other invertebrates (Wimp and Whitham, 2001; Dejean and Corbara, 2003; Blüthgen et al., 2004b; Mody and Linsenmair, 2004), since honeydew is one of the most important resources of large dominant ant colonies in rainforest vegetation (Blüthgen et al., 2003; Davidson et al., 2003).

The number of ant workers per individual hemipteran may be a meaningful measure of the quality or productivity of each trophobiosis. For the broad spectrum of species examined in this study, this ant/hemipteran ratio decreased as the number of hemipterans in the association increased. This pattern may be widespread and was found in several systems elsewhere (Breton and Addicott, 1992; Morales, 2000; Shingleton and Foster, 2000; Blüthgen and Fiedler, 2002), although some studies showed indirect evidence for an increased intensity of ant attendance with increasing number of hemipterans (Wood, 1982; Cushman and Whitham, 1989; Itioka and Inoue, 1996). In many cases where the number of ant workers per individual hemipteran is small, owing to large numbers of the latter or to competition with neighbouring hemipteran aggregations for a limited number of ants, hemipterans suffer from an increased risk of predation or parasitism (Cushman and Whitham, 1991; Breton and Addicott, 1992; Morales, 2000; Shingleton and Foster, 2000; Fischer et al., 2001). In addition, ant partners may vary in

their protective effectiveness (Buckley and Gullan, 1991; Gullan, 1997; Itioka and Inoue, 1999). Our study shows that several common features can be found among ants across a highly diverse spectrum of trophobiotic associations, such as an increased recruitment to larger trophobioses at a declining relative rate, effective monopolisation against competitors and continuity of attendance at least in larger trophobioses. This emphasises the importance of honeydew as a food source for these tropical ant species.

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