

Bottom-up control and co-occurrence in complex communities: honeydew and nectar determine a rainforest ant mosaic

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Complex distribution patterns of species-rich insect communities in tropical rainforests have been intensively studied, and yet we know very little about processes that generate these patterns. We provide evidence for the key role of homopteran honeydew and plant nectar in structuring ant communities in an Australian tropical rainforest canopy and understorey. We also test the ant visitation of these resources against predictions derived from the ‘ant-mosaic’ hypothesis. Two ant species were highly dominant in terms of territorial behaviour and abundance: *Oecophylla smaragdina* and *Anonychomyrma gilberti*. Both dominant ant species monopolised large aggregations of honeydew-producing homopterans. Attended homopteran species were highly segregated between these two ant species. For the use of extrafloral and floral nectar (involving 43 ant species on 48 plant species), partitioning of ant species among plant species and between canopy and understorey was also significant, but less pronounced. In contrast to trophobioses, simultaneous co-occurrence of different nectar foraging ant species on the same plant individuals was frequent (23% of all surveys). While both dominant ant species were mutually exclusive on honeydew and nectar sources, co-occurrence with non-dominant ant species on nectaries was common. The proportion of visits with co-occurrences was low for dominant ants and high for many subordinate species. These findings support the ant mosaic theory. The differential role of honeydew (as a specialised resource for dominant ants) and nectar (as an opportunistic resource for all ants including the co-occurring non-dominant species) provides a plausible structuring mechanism for the Australian canopy ant community studied.

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The structure of plant and animal communities is a product of multiple interacting processes, including ‘top-down effects’ through predation versus ‘bottom-up effects’ through resource availability (Hunter and Price 1992), or stochastic recruitment following disturbance regimes versus competition and niche differentiation (Tilman 1982, Hubbell et al. 1999). Yet, for complex communities in tropical ecosystems, we have only limited understanding about the extent to which coexistence can

be attributed to habitat and resource heterogeneity or actual interspecific competition.

Ant communities have been the focus of many studies, because of their extraordinary abundance and primary ecological function (Hölldobler and Wilson 1990, Stork 1991) and hence economic importance (Way and Khoo 1992). Both exploitation and interference competition can be pronounced and strongly asymmetric between ant species (Fellers 1987, Savolainen and Vepsäläinen 1988,

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Andersen 1992, Andersen and Patel 1994, Perfecto 1994). In structurally simple tropical plantations a small number of dominant ant species was commonly found to maintain mutually exclusive territories, a community structure that has been termed 'ant mosaic' (Leston 1970, Room 1971, Majer 1972). Ant mosaics have since then been reported from all tropical continents (Jackson 1984a, Majer 1993, Dejean and Corbara 2003), although their structural importance in undisturbed mature rainforests has been questioned (Dejean et al. 2000, Floren and Linsenmair 2000). Besides the mutually exclusive distribution of dominant ants, an important second prediction is that in ant mosaics a specific set of ant species co-occurs with each of the dominant species (Room 1971, 1975, Majer 1976, Taylor and Adedoyin 1978). These patterns may be behaviourally controlled by different tolerance levels among ant species for species-specific olfactory or tactile signals, defensive strategies or spatio-temporal avoidance (Majer 1976, Hölldobler and Wilson 1990, Davidson 1998, Mercier et al. 1998). However, it is not known whether this tolerance mirrors a reduced resource overlap and interspecific competition. The distribution of sub-dominant ants may be controlled by the dominant species as suggested by the ant mosaic hypothesis, but the same pattern may also be caused by colonisation events (Yu et al. 2001), or by a heterogeneous environment when co-occurring 'dominant' and 'sub-dominant' ants share the same resource or habitat preferences. Many ant community analyses focused on spatial patterns by using invasive sampling techniques, such as canopy fogging (Stork 1991, Floren and Linsenmair 1997, 2000). Spatial or temporal patterns in insect samples may or may not reveal the presence of underlying processes and depend on the appropriate scale applied. The statistical tools used to indirectly infer effects of competition have been subject to controversial debate for a long time and are highly dependent on the null models chosen (Gotelli and Graves 1996, Gotelli 2000). In contrast, information about the actual resource distribution and use is scarce, particularly from forest canopies (Lowman and Nadkarni 1995, Stork et al. 1997, Blüthgen et al. 2000b, Dejean et al. 2000, Yanoviak and Kaspari 2000). A resource-based approach may enable us to understand not only the spatial consequences of, but also the mechanisms behind, community structures.

Establishment and maintenance of territories, as in ant mosaics, is a costly strategy, involving worker losses through fights, guard ants, and mass-recruitment systems (Hölldobler and Lumsden 1980, Hölldobler and Wilson 1990). The availability of a stable and rewarding resource supply worth defending may thus be crucial (Jackson 1984b). Recently it has been shown that plant and herbivore exudates represent such key resources for arboreal ants (Tobin 1995, Davidson 1997, Blüthgen et al. 2000b, 2003, Davidson et al. 2003).

In this study, we examined a diverse spectrum of plant sap sources visited by ants within an Australian tropical rainforest in order to analyse (1) the degree of resource partitioning or specialisation among ants on plants, (2) the extent of resource monopolisation versus ant species co-occurrence or dynamic turnover on resources, and (3) the consequences of these patterns of resource use for the structure and distribution of tropical ant communities particularly in the context of ant mosaic theories. Ant preferences for sugar and amino acid composition of experimental and natural nectar sources, and consequences for interspecific competition will be presented elsewhere (Blüthgen and Fiedler 2004a, 2004b).

Material and methods

Study site

This study was carried out in the rainforest at the Australian Canopy Crane in Cape Tribulation, Far North Queensland, Australia (16°07'S, 145°27'E, 80 m a.s.l.) and adjacent forests within 5 km radius of the crane site including patches of open secondary forest. The rainforest is characterised by a high abundance of lianas and an average canopy height of 25 m (complex mesophyll vine forest, Tracey 1982). Average rainfall is about 3500 mm per year, 60% of which occurs in the wet season between December and March. Mean daily temperature ranges from 22°C (July) to 28°C (January) (Turton et al. 1999). The study was conducted for 19 months (September 1999–May 2000, January–August 2001, March–May 2002). During this time, most parts of the forest have been in an early stage of recovery from category 3 cyclone 'Rona' in February 1999 when large parts of the canopy were severely damaged. Due to canopy gaps, the forest structure within and outside the crane site was highly heterogeneous.

Sampling methods

We surveyed nectar and honeydew sources for their attendance by ants, including honeydew excreted by homopterans, nectar secretions of caterpillars, plant wound sap, and extrafloral and floral nectaries (EFNs and FNs hereafter). Surveys included plant species known to provide nectar, but also novel cases where the activity of ants itself attracted our attention to these sources (Blüthgen and Reiferrath 2003, Blüthgen et al. 2004). Both understorey (height above ground < 3 m; observed from the ground) and canopy level (height 10–34 m) were included. Canopy observations were performed with the aid of the canopy crane (48.5 m tall with a jib length of 55 m) and thus restricted to the area covered by the crane (0.95 ha). Understorey plants were

recorded in a more extended study area (above) including the crane site and adjacent forests. Observed plants were haphazardly selected within the study area and irregularly distributed throughout the forest, especially along paths and in more accessible areas. We attempted to represent the widest possible spectrum of plant species with ant-tended sources. However, no complete survey was attempted within an area, and replications of the same associations in close proximity were avoided (below). Individual plants were labelled to allow repeated observations. For each survey, we recorded the identity and number of ants when they consumed nectar or honeydew in the observable area of these plants, typically including the entire foliage on small understorey shrubs and entire palm inflorescences but often only accessible and exposed parts of the tree canopies or climbing plants. Observations were completed within ca 1–2 minutes per understorey plant, or 5–10 min in tree canopies although surveys of homopterans in some of the trees involved up to several hours each. Hence, each survey represents a random ‘snapshot’ of simultaneous ant activity on plants rather than a complete record of the assemblage. Surveys in the understorey were performed during the day and night (07 h–01 h), but canopy observations were limited to daytime for logistical reasons (07 h–18 h). Nectar secretion of all EFNs and FNs was confirmed by glucose indicator paper (Glucostix®, Bayer), hand-held refractometer and/or HPLC (analyses are presented in Blüthgen et al. 2004). Vouchers of all ant and homopteran species were collected and subsequently identified at the Australian National Insect Collection and/or by taxonomic specialists. Ant nomenclature follows recent literature (Shattuck 1999, Kohout 2000). Three largely nocturnal *Camponotus* species and all coccoids from several families were pooled in association analyses, because not all cases were collected and identified. For ant species richness estimates, it was assumed that two of the three *Camponotus* species occurred only in a single sample each.

Data analyses

For analysis of associations between ants and plants, a contingency table of ant × plant species was used with frequencies of interactions as cell entries. In order to ensure independence of observations in this table (attempting to avoid pseudoreplication within territories of single ant colonies), the following rules applied: only those observations were considered that were either more than 8 m apart from their nearest neighbour on the ground or on different, unconnected tree crowns in the canopy, or that involved different ant and/or plant species; repeated observations on labelled plants were collapsed into one data point for each plant individual.

This method resulted in a conservative estimate of actual quantitative preference patterns, particularly where repetitions are rejected or species turnover is pronounced.

The degree of interaction specificity between ants and nectar/honeydew sources was examined using two approaches:

(1) a randomisation test of the contingency tables (equivalent to chi-square tests) was performed using an algorithm based on the matrix statistic

$$T = \sum_i \sum_j (a_{ij} \log a_{ij})$$

where a_{rc} are the observation frequencies in the matrix of i rows and j columns (Blüthgen et al. 2000a; program available at <http://itb.biologie.hu-berlin.de/~nils/stat/>) (10,000 randomisations performed). Inference on statistical significance is based on the proportion of randomisations that produce data distributions equal to or more homogeneous than the observed empirical value (randomly generated and observed T statistics are denoted as T_{ran} vs T_{obs} , respectively).

(2) For a more detailed analysis of patterns in the ant-plant association matrix, a correspondence analysis (CA) was performed using Statistica 5.5 for Windows (StatSoft, Inc.; Tulsa, OK, USA) on the reduced contingency table of associations between ants and nectar plants (22 ant × 23 plant species, each with ≥ 5 observed interactions). Coordinates for the first two dimensions extracted by CA were used for testing differences in plant preferences between a priori defined groups of ants (canopy vs understorey, sub-familii, co-occurrence with dominant ants), and of ant visitor spectra between plant groups (canopy vs understorey, FNs vs EFNs, plant life forms), performing one-factorial multiple analyses of variance (MANOVA) for each comparison. The significance level was adjusted by sequential Bonferroni correction (Hochberg 1988).

The number of ant species that foraged simultaneously on the respective resource type on the same plant individual were counted and denoted as S . Ant species co-occurrence was defined as the proportion of plant surveys where $S > 1$. The proportion of visits with co-occurrences was calculated only for those cases where at least two ant workers were present on a plant. The distribution of co-occurrences between particular ant species was obtained using a reduced dataset excluding replications of interactions from the same plant or area (8 m radius). A test for randomness of these co-occurrence patterns was calculated using EcoSim (Gotelli and Entsminger 2001; 50,000 randomisations). We chose the C-score index (Stone and Roberts 1992) and fixed row and column totals (Ribas and Schoereder 2002), but conclusions based on other indices were the same (data not shown).

Ant species replacement (R_s) between consecutive surveys was calculated for all plants that were repeatedly surveyed using the following index:

$$R_s = \frac{e_1}{S_1} \times \frac{e_2}{S_2}$$

where e_1 and e_2 represent the number of species that were exclusively found during the earlier and later survey, and S_1 and S_2 the total number of species found during the earlier and later survey, respectively. Thus R_s ranges between zero (when none of the two surveys has exclusive species) and one (when no species overlap is found). The frequency of replacement is the percentage of surveys where $R_s > 0$. Only consecutive positive records were compared by this equation, i.e. surveys on plants where no ant was found were skipped. An estimate of the species richness based on randomised species accumulation curves was performed for the number of ant species on nectar and honeydew sources (incidence-based), respectively, using the program EstimateS 6.0b1 (Colwell 2001; 'Chao2' estimator; 100 randomisations).

Results

Ant community structure

In total, 43 ant species were found to feed on nectar sources including six species that also foraged for honeydew (Table 1). Estimated ant species richness (\pm SD) is 44 (\pm 2) on nectaries and 6 (\pm 0) on honeydew sources (EstimateS; Chao2), thus records of ants on nectaries represent nearly the entire expected species pool based on accumulation curves, and no further species at honeydew sources are expected. Twenty-five ant species were found in the canopy and 40 in the understorey (estimated ant species richness for each stratum: 28 (\pm 5) and 46 (\pm 7), respectively). Species richness and composition of nectar feeding ant assemblages are comparable to ant collections from two canopy foggings each in a 10 \times 10 m area close to the study site (Majer et al. 2001 a total of 38 and 44 species, respectively). Most ant species typically dwell in arboreal nests (both living or dead plant material), although several species nest in dead wood both on trees and the ground, and several ground-nesting species are also involved (Table 1). The two most dominant ants in the study site were *Oecophylla smaragdina* (weaver ants) and *Anonychomyrma gilberti*, characterised by very large colonies that maintain mutually exclusive territories. Extensive combats between these two species were observed on three occasions (but never between other ants in the study site). *Oecophylla* ants build nests using leaves from a great variety of trees and lianas in the upper canopy level (Blüthgen and Fiedler 2002). *Anonychomyrma* nests were only found in trunks of one common tree species, *Syzygium 'erythrocalyx'* (Monteith 1986). The activity of large colonies of both species extended over a large area in the understorey and

into the crowns of several adjacent trees. The two dominant ants were the most frequent visitors on a broad spectrum of nectar sources (besides *Crematogaster cf. fusca*) and honeydew (Table 1). Co-occurrences between different ant species on the same plant were common (below), but not equally common between different pairs of ant species (Table 2). The two dominant ants were never found nectar foraging on the same plant. However, several non-dominant ant species commonly shared the same plants with the dominants. These associated species pools differed to a large extent between the two dominants despite some overlap, and this compartmentalisation was significantly different from random associations (randomisation test: $T_{\text{obs}} = 148$, mean \pm SD $T_{\text{ran}} = 134 \pm 3$, $p < 0.001$). Four categories can be recognised: (1) several species were commonly found in territories of *Oecophylla*, but rarely or never with *Anonychomyrma*. (2) Some species commonly co-occurred with both dominant species, while (3) others were found to co-occur more frequently with *Anonychomyrma*, and (4) for some species, co-occurrences with dominant ants were rare. Note that this classification is not distinct rather than continuous; for the categories shown in Table 2, ants were assigned to group (4) when fewer than two co-occurrences with dominants were found and to (2) when the ratio of co-occurrences with *Oecophylla* vs *Anonychomyrma* was between 1:3 and 3:1. The co-occurrence matrix used here (Table 2) is derived only from visitation of EFNs and FNs, but other observations and experiments involving artificial nectaries strongly support this classification scheme (N. Blüthgen, unpubl.). Most ants from both (1) and (2) were regularly observed to share the same trails on trunks and branches used by *Oecophylla* without any aggressive interaction (Table 2). The C-score of ant species co-occurrence (234.6) is higher than that of randomly generated matrices (mean \pm SD: 232.7 ± 0.8 , $p < 0.01$), which would be expected when competition or other processes structure the ant community (Stone and Roberts 1992, Gotelli 2000, Ribas and Schoereder 2002).

Extrafloral and floral nectaries

Thirty-four plant species with active EFNs were observed in the study site (Table 3; representing ca 17% of larger tree species and 21% of the climbing plant species checked, see Blüthgen and Reifenrath 2003 for complete list and details about their structure and distribution). All nectar feeding ant species in this study (except for one *Podomyrma* species observed on a single flowering tree) were observed on EFNs (Table 1). On all EFN-bearing plant species, ants were the most common nectar consumers and constituted more than 90% of the total arthropod individuals observed feeding. Flower nectar use by ants was recorded on 14 plant species (Table 3),

Table 1. Ant species feeding on extrafloral nectaries (EFNs), floral nectaries (FNs), and honeydew, their nest sites, stratification and daytime activity. Typical nest sites: (a) arboreal and (g) ground nests. Numbers are frequencies of spatially independent occurrences or interactions with different plant species. Significant overrepresentation of understorey vs canopy or diurnal vs nocturnal activity is marked with (*) (χ^2 -test against expected values from proportions of total ant visits (column totals); applied to all species with ≥ 5 observations, significant differences after sequential Bonferroni correction underlined). The last column shows the number of plant species visited for nectar.

| Ant species | Nest | Stratum ¹⁾ | | Activity ²⁾ | | Resources | | | |
|--|------|-----------------------|--------|------------------------|-------|-----------|-----|-----------|------------|
| | | Under-storey | Canopy | Day | Night | EFNs | FNs | Honey dew | Plant spp. |
| DOLICHODERINAE | | | | | | | | | |
| <i>Anonychomyrma gilberti</i> (Forel) | a | 25 | 40* | 38* | 1 | 59 | 6 | 9 | 20 |
| <i>Leptomyrmex unicolor</i> Emery | g | 5 | 11* | 5 | – | 8 | 8 | – | 9 |
| <i>Tapinoma melanocephalum</i> (Fabricius) | g | 10* | – | 10 | 3 | 10 | – | – | 8 |
| <i>Tapinoma minutum</i> Mayr | – | 3 | – | 3 | – | 3 | – | – | 3 |
| <i>Technomyrmex albipes</i> (Smith) | a | 31* | 6 | 31 | 5 | 35 | 2 | 9 | 14 |
| <i>Turneria bidentata</i> Forel | a | 1 | 11* | 1 | – | 9 | 3 | – | 6 |
| FORMICINAE | | | | | | | | | |
| <i>Camponotus</i> ‘nocturnal’ (3 spp.) ⁴⁾ | ag | 8* | – | – | 9* | 8 | – | – | 6 |
| <i>Camponotus</i> sp1 (<i>macrocephalus</i> gp.) | a | 5 | – | 5 | – | 5 | – | – | 3 |
| <i>Camponotus</i> sp6 (<i>gasseri</i> gp.) | – | – | 1 | – | – | 1 | – | – | 1 |
| <i>Camponotus vitreus</i> (Smith) | a | 14 | 9 | 13 | 1 | 22 | 1 | – | 13 |
| <i>Echinopla australis</i> Forel | a | 1 | 1 | 1 | – | 2 | – | – | 2 |
| <i>Oecophylla smaragdina</i> (Fabricius) | a | 32 | 65* | 29 | 4 | 71 | 26 | 44 | 26 |
| <i>Paratrechina minutula</i> (Forel) | ag | 4 | 1 | 5 | – | 5 | – | – | 5 |
| <i>Paratrechina vaga</i> (Forel) | ag | 34* | – | 29 | 12* | 34 | – | 5 | 12 |
| <i>Polyrhachis</i> (<i>Cyrtomyrma</i>) ‘Cyrt0 03’ Kohout | a | 5 | 5 | 5 | – | 7 | 3 | – | 7 |
| <i>Polyrhachis</i> (<i>Cyrtomyrma</i>) ‘Cyrt0 06’ Kohout | a | 1 | 3 | 1 | – | 3 | 1 | – | 4 |
| <i>Polyrhachis</i> (<i>Cyrtomyrma</i>) ‘Cyrt0 08’ Kohout | a | 2 | 1 | 2 | – | 2 | 1 | – | 3 |
| <i>Polyrhachis</i> (<i>Cyrtomyrma</i>) ‘NB5041’ Kohout | a | 7 | 8 | 9 | – | 15 | – | – | 8 |
| <i>Polyrhachis</i> (<i>Cyrtomyrma</i>) <i>yorkana</i> Forel | a | 6 | 4 | 7 | – | 9 | 1 | – | 8 |
| <i>Polyrhachis</i> (<i>Hagiomyrma</i>) <i>thusnelda</i> Forel | a | – | 2 | – | – | 1 | 1 | – | 2 |
| <i>Polyrhachis</i> (<i>Hedomyrma</i>) <i>cupreata</i> Emery | a | 1 | 1 | 1 | – | 2 | – | – | 2 |
| <i>Polyrhachis</i> (<i>Myrma</i>) <i>foreli</i> Kohout | a | 3 | 38* | 3 | – | 24 | 17 | – | 15 |
| <i>Polyrhachis</i> (<i>Myrmhopla</i>) <i>mucronata</i> Smith | a | 1 | 1 | – | 1 | 2 | – | – | 2 |
| <i>Polyrhachis</i> (<i>Myrmotherinx</i>) <i>delicata</i> Crawley | a | 1 | – | – | 1 | 1 | – | – | 1 |
| MYRMICINAE | | | | | | | | | |
| <i>Crematogaster</i> cf. <i>fusca</i> Smith | a | 64* | 17 | 68* | 3 | 77 | 4 | 3 | 24 |
| <i>Crematogaster</i> cf. <i>pythia</i> Forel | a | 28 | 14 | 22 | 8 | 40 | 2 | – | 16 |
| <i>Crematogaster</i> sp3 | a | 6 | – | 7 | – | 6 | – | – | 4 |
| <i>Monomorium fieldi</i> var. <i>laeve nigrius</i> Forel | – | 2 | – | 3 | – | 2 | – | – | 2 |
| <i>Monomorium floricola</i> Forel | a | 21* | 5 | 20 | 1 | 23 | 3 | – | 13 |
| <i>Pheidole</i> cf. <i>athertonensis</i> | g | 3 | – | 3 | – | 3 | – | – | 3 |
| <i>Pheidole impressiceps</i> Mayr | g | 4 | – | 4 | – | 4 | – | – | 3 |
| <i>Pheidole platypus</i> Crawley | g | 29* | 2 | 32 | 5 | 31 | – | – | 10 |
| <i>Pheidole</i> sp1 | g | 4 | – | 2 | 2 | 4 | – | – | 4 |
| <i>Podomyrma</i> sp1 | – | – | 1 | – | – | – | 1 | – | 1 |
| <i>Rhoptromyrmex wroughtonii</i> Forel | g | 11* | – | 8 | 6* | 11 | – | 11 | 6 |
| <i>Strumigenys guttulata</i> Forel | g | 1 | – | 3 | – | 1 | – | – | 1 |
| <i>Tetramorium insolens</i> F.Smith | g | 3 | – | – | 3 | 3 | – | – | 3 |
| <i>Tetramorium validiusculum</i> Emery | g | 16* | – | 8 | 9* | 16 | – | – | 8 |
| PONERINAE | | | | | | | | | |
| <i>Odontomachus ruficeps</i> Smith | g | 2 | – | 1 | 1 | 2 | – | – | 1 |
| <i>Rhytidoponera spoliata</i> (Emery) | g | 2 | – | 2 | – | 2 | – | – | 2 |
| PSEUDOMYRMECINAE | | | | | | | | | |
| <i>Tetraponera nitida</i> (Smith) | a | 2 | 5 | 2 | – | 6 | 1 | – | 6 |
| Total (median): | | 398 | 252 | 383 | 75 | 569 | 81 | 81 | (5) |

¹⁾ Restricted to visitation of EFNs and FNns only (n = 432 plant individuals).

²⁾ Activity data restricted to nectar use in the understorey, including multiple surveys per plant (n = 417 plant surveys).

³⁾ Only for species with ≥ 5 observations.

⁴⁾ Includes three similar nocturnal species that were not always collected and identified (2 spp. from *C. novae-hollandiae* group and *C. (Colobopsis) macrocephalus* (Erichson)).

involving most ant species common in the canopy (total 17 ant species; Table 1). Additional 12 flowering plant species were checked but did not show any floral nectar use by ants (five of them had very narrow corolla tubes that were inaccessible to most ants) (Blüthgen et al.,

2004). The total number of plant individuals and species offering floral nectar to ants was much smaller than for extrafloral nectar during the study (Table 3), and for any species, the flowering period was much shorter than the usual availability of extrafloral nectar. In contrast to

Table 2. Frequency of co-occurrence between the nectar foraging ant species on the same individual plant (interaction frequencies > 3 boldface). Species ordered by total interaction frequency (only those with totals > 3 shown; empty columns removed). Ant mosaic categories were classified into four groups: co-occurrence in territories of (1) *Oecophylla*, (2) both *Oecophylla* and *Anonychomyrma*, (3) *Anonychomyrma*; all other species were assigned to category (4) (see text). An asterisk (*) marks ants that were commonly observed to share trails with *Oecophylla*.

| Ant species | Mosaic | Pol. for. | Oec. sma. | Cre. pyt. | Cre. fus. | Cam. vit. | Ano. gll. | Pol. CyNB | Tur. bid. | Tec. alb. | Tet. nit. | Mon. flo. | Pol. Cy3 | Lep. uni. | Par. vag. | Phe. pla. |
|-----------------------------------|--------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|-------------|--------------|--------------|--------------|
| <i>Polyrhachis foreli</i> | 2* | • | | | | | | | | | | | | | | |
| <i>Oecophylla smaragdina</i> | 1 | 14 | • | | | | | | | | | | | | | |
| <i>Crematogaster cf. pythia</i> | 1* | 6 | 12 | • | | | | | | | | | | | | |
| <i>Crematogaster cf. fusca</i> | 1* | 7 | 11 | 1 | • | | | | | | | | | | | |
| <i>Camponotus vitreus</i> | 2* | 5 | 5 | 7 | 6 | • | | | | | | | | | | |
| <i>Anonychomyrma gilberti</i> | 3 | 5 | — | — | 2 | 2 | • | | | | | | | | | |
| <i>Polyrhachis Cyrtio</i> NBS041* | 3 | 5 | 1 | 1 | 2 | 3 | 7 | • | | | | | | | | |
| <i>Turnera bidentata</i> | 2 | 4 | 3 | 4 | — | 2 | 1 | 2 | • | | | | | | | |
| <i>Tetramymex albipes</i> | 4 | 3 | 1 | 3 | 1 | 4 | — | 1 | — | • | | | | | | |
| <i>Tetraponera nitida</i> | 1* | 4 | 5 | 3 | 1 | 2 | — | 1 | 1 | — | • | | | | | |
| <i>Monomorium floricola</i> | 4 | 1 | — | 1 | — | 1 | — | — | 2 | 1 | — | • | | | | |
| <i>Polyrhachis Cyrtio</i> 3 | 2 | 2 | 1 | 1 | 3 | — | 3 | — | 1 | 1 | 1 | 2 | • | | | |
| <i>Leptonymex unicolor</i> | 2 | 4 | 3 | 1 | 1 | 1 | 1 | — | — | 1 | — | — | 1 | • | | |
| <i>Paratrechina vaga</i> | 4 | — | — | 3 | — | — | — | — | — | 2 | — | — | — | — | • | |
| <i>Pheidole platypus</i> | 1* | 1 | 2 | 1 | 1 | — | — | — | — | — | — | — | — | — | 3 | • |
| <i>Paratrechina minutula</i> | 4 | 1 | — | — | 1 | — | 1 | — | 1 | — | — | 2 | 1 | — | — | — |
| <i>Polyrhachis yorikana</i> | 2 | — | 1 | 2 | 1 | — | 1 | — | — | 1 | — | — | — | — | — | — |
| <i>Tapinoma melanocephalum</i> | 4 | — | — | 1 | 1 | — | — | — | — | — | — | 1 | — | — | 2 | — |
| <i>Camponotus</i> sp1 | 4 | — | — | 1 | — | 1 | — | — | — | 1 | — | 1 | — | — | — | — |
| <i>Polyrhachis Cyrtio</i> 6 | 3 | — | — | — | — | — | 3 | — | — | — | — | 1 | — | — | — | — |
| <i>Tapinoma minutum</i> | 4 | — | — | — | — | — | — | — | — | — | — | 1 | — | — | 1 | 1 |

Table 3. Plant species with (a) extrafloral nectaries and (b) floral nectaries visited by ants; (a) reduced to species where five or more interactions have been observed (for the remaining ones, see Blüthgen and Reifenrath 2003). Life-form: cl = climbing plant, sh = shrub (incl. small trees < 5 m), tr = tree, pa = palm. Stratum: c = canopy, u = understorey, + = observations of nocturnal nectary activity. N = Number of plant individuals with positive observations of ant visits.

| Family | Species | Life-form | Stratum | N |
|--------------------------|--|-----------|------------------|----|
| a) Extrafloral nectaries | | | | |
| ASCLEPIADACEAE | <i>Wrightia laevis</i> subsp. <i>millgar</i> (Bailey) Ngan | tr | c | 2 |
| | <i>Ichnocarpus frutescens</i> R.Br. | cl | c | 9 |
| CONVOLVULACEAE | <i>Ipomoea indica</i> (Burm.) Merr. | cl | u ⁺ | 19 |
| | <i>Merremia peltata</i> Merr. | cl | u ⁺ c | 67 |
| EUPHORBIACEAE | <i>Endospermum myrmecophilum</i> L.S.Sm. | tr | u ⁺ | 11 |
| | <i>Glochidion philippicum</i> (Cav.) C.B.Rob. | tr | c | 1 |
| | <i>Homalanthus novoguineensis</i> (Warb.) K.Schum. | sh | u ⁺ | 28 |
| | <i>Macaranga involucreata</i> subsp. <i>mallotoides</i> (F.Muell.) L.M.Perry | sh | u ⁺ | 45 |
| | <i>Mallotus mollissimus</i> (Geiseler) Airy Shaw | sh | u | 4 |
| | <i>Rockinghamia angustifolia</i> (Benth.) Airy Shaw | tr | u c | 7 |
| FABACEAE s.l. | <i>Castanospermum australe</i> A.Cunn. & Fraser ex Hook | tr | c | 4 |
| | <i>Entada phaseoloides</i> Merr. | cl | u ⁺ c | 27 |
| FLAGELLARIACEAE | <i>Flagellaria indica</i> L. | cl | u ⁺ c | 79 |
| LAMIACEAE | <i>Clerodendrum tracyanum</i> (F.Muell.) F.Muell. ex Benth. | sh | u | 5 |
| MELIACEAE | <i>Dysoxylum pettigrewianum</i> F.M.Bailey | tr | u c | 9 |
| MYRSINACEAE | <i>Ardisia pachyrrhachis</i> (F.Muell.) F.M.Bailey | sh | u ⁺ | 17 |
| MYRTACEAE | <i>Syzygium 'erythrocalyx'</i> B.Hyland | tr | u ⁺ c | 14 |
| SMILACACEAE | <i>Smilax cf. australis</i> | cl | u ⁺ | 6 |
| (b) Floral nectaries | | | | |
| ARECACEAE | <i>Archontophoenix alexandrae</i> (F.Muell.) H.Wendl. & Drude ¹⁾ | pa | c | 3 |
| | <i>Licuala ramsayi</i> (F.Muell) Domin | pa | c | 6 |
| | <i>Normanbya normanbyi</i> (W.Hill) L.H.Bailey ¹⁾ | pa | c | 12 |
| BIGNONIACEAE | <i>Neosepicea jucunda</i> (F.Muell.) Steenis | cl | c | 1 |
| ELAEOCARPACEAE | <i>Elaeocarpus angustifolius</i> Blume | tr | c | 3 |
| EUPHORBIACEAE | <i>Rockinghamia angustifolia</i> (Benth.) Airy Shaw | tr | c | 1 |
| FABACEAE s.l. | <i>Entada phaseoloides</i> Merrill | cl | c | 6 |
| LAURACEAE | <i>Cryptocarya hypospodia</i> F.Muell. | tr | c | 1 |
| | <i>Cryptocarya murrayi</i> F.Muell. | tr | c | 4 |
| MELIACEAE | <i>Dysoxylum mollissimum</i> subsp. <i>molle</i> (Miq.) D.J.Mabberley | sh | u | 1 |
| | <i>Dysoxylum papuanum</i> Mabb. | tr | c | 2 |
| | <i>Toona ciliata</i> M.Roem | tr | c | 1 |
| MENISPERMACEAE | <i>Pachygone longifolia</i> F.M.Bailey | cl | c | 3 |
| | <i>Stephania japonica</i> (Thumb.) Miers | cl | c | 1 |
| MYRSINACEAE | <i>Ardisia pachyrrhachis</i> (F.Muell.) F.M.Bailey | sh | u | 1 |
| | <i>Embelia caulialata</i> S.T.Reynolds | cl | c | 1 |
| OLEACEAE | <i>Jasminum didymum</i> G.Forst ²⁾ | cl | c | 1 |

¹⁾ including wound sap, ²⁾ postfloral nectar.

EFNs, ants constituted usually only a minority of the total arthropod flower visitors observed. For the scope of this paper, sap-secreting wounds in the foliage of *Cardwellia sublimis* and *Syzygium sayeri* trees were categorised as (functional) EFNs; ant attendance of wound secretions on palm inflorescences (e.g. from flower abscission scars on *Normanbya normanbyi*) were pooled with true flower nectar use in these plants, and postfloral nectar of *Jasminum didymum* was available to ants after corolla abscission (Blüthgen et al., 2004).

The distribution of nectar-feeding ant species on plant species was significantly different from random ($T_{\text{obs}} = 807$, $\text{mean} \pm \text{SD}$ $T_{\text{ran}} = 703 \pm 13$, $p < 0.001$). Because $T_{\text{obs}} > T_{\text{ran}}$, the ant-plant matrix can be considered compartmentalised, i.e. ant species were significantly partitioned across plant species. Nevertheless, overlap between plant species used was common, and a broad range of EFN- and FN-plants was usually visited by each ant species (median: 5, quartiles: 2–9, Table 1).

Factorial effects in the ordination of ant plant associations are summarised in Table 4. No significant segregation of ant sub-families was found and no significant separation of ant species that were involved in trophobiosis or not. Between ant mosaic compartments (common co-occurrence with either *Oecophylla* or *Anonychomyrma* or both; categories 1–3, above) there was no significant effect. However, those ant species that were rarely found to co-occur with the dominant ants (category 4) were significantly segregated from the rest (categories 1–3). Moreover, there was a clear effect of vertical stratification, with ants foraging predominantly in the canopy being significantly (but not entirely) separated from those seen nectar foraging in the understorey (Table 4a). Consequently, vertical stratification was also found to significantly separate nectary-bearing plant species groups in regard to their ant visitation spectrum (Table 4b). Extrafloral and floral nectaries also differed significantly in their ant assemblage (excluding understorey plants; no flowers in the understorey were common that were visited by ants, so interactions

Table 4. Multiple one-way analyses of variance (MANOVA) for effects of a priori classes on first two dimensions from correspondence analysis (explanatory power: 26.4% and 13.9%, respectively); (a) differences between plants in ant visitation spectra, and (b) between ants in plant preferences. Significant effects after Bonferroni correction in boldface.

| Effect | Rao's R | df ₁ | df ₂ | p |
|---|---------|-----------------|-----------------|----------------|
| (a) Ants | | | | |
| Stratum: canopy or understorey | 10.7 | 2 | 19 | < 0.001 |
| Sub-family ¹⁾ | 1.0 | 4 | 34 | 0.44 |
| Trophobiosis ²⁾ | 1.4 | 2 | 19 | 0.27 |
| With dominant ants or not ³⁾ | 6.7 | 2 | 19 | 0.006 |
| Dominant ant affiliation ⁴⁾ | 1.0 | 4 | 18 | 0.45 |
| (b) Plants | | | | |
| Stratum: canopy, understorey or both | 8.9 | 4 | 38 | < 0.001 |
| Nectary: EFN or FN ⁵⁾ | 7.4 | 2 | 12 | 0.008 |
| Life form: tree or liana ⁵⁾ | 0.4 | 2 | 12 | 0.69 |

¹⁾ only Dolichoderinae, Formicinae and Myrmicinae.

²⁾ ant species observed to be involved in trophobiosis in the study area or not.

³⁾ common co-occurrence with *Oecophylla* or *Anonychomyrma* (both species included) or not (categories 1–3 vs 4, see text).

⁴⁾ common co-occurrence with either *Oecophylla* or *Anonychomyrma* (both species included) or both (categories 1, 2 and 3).

⁵⁾ excluding understorey plants.

between stratification and type of nectaries could not be tested). No significant segregation was found between nectar feeding ant communities on canopy trees and lianas. Inference about significant differences between groups did not change when one or three ordination dimensions were used, or when a larger association matrix was used (29 ant \times 32 plant species, ≥ 3 interactions); for a reduced table (14 \times 13 species, ≥ 10 interactions), only the stratification effects were significant (results not shown).

Stratification of nectar-foraging ants between canopy and understorey was also pronounced when all nectar resources were considered (irrespective of plant species identities considered in the CA above), and highly significant in a randomisation test (Table 1; $T_{\text{obs}} = 1960$, $T_{\text{ran}} = 1838 \pm 5$, $p < 0.001$). Four species showed a significantly higher nectar foraging activity in the canopy, including the two dominant ants *A. gilberti* and *O. smaragdina*, and four species were significantly more active in the understorey (compared to expected values based on the totals; Table 1). This suggests that, as far as ant species foraging for nectar is concerned, stratification at the Australian study site includes a differential stratum-specific activity in a few (common) ant species and a restriction to foraging near ground level by a considerable proportion of the ant fauna (half of the ant species recorded).

EFNs from all plant species were active during the day, but nocturnal secretory activity was also confirmed for all common species observable from the ground (Table 3). Thus EFN secretion may be assumed to be continuous, though not necessarily constant, in most if not all plants at the Australian study site. Most common ants also proved to be active during day and night (Table 1, note that most surveys were during the day). Differentiation of all ant species on EFNs between day and night was significant ($T_{\text{obs}} = 1292$, $T_{\text{ran}} = 1248 \pm 4$, $p < 0.001$). However, only few species deviated signifi-

cantly from the total activity pattern, most notably a pooled group of nocturnal *Camponotus* species (Table 1).

Honeydew

Only six ant species were found in direct trophobiotic association with honeydew-producing homopterans or lycaenid caterpillars (Table 5). The same ant species were among the most common visitors of EFNs and FNs (Table 1). Aside from the dominant ants *Oecophylla* and *Anonychomyrma*, the other common trophobioses involved three ant species that rarely co-occurred with the dominants (category 4 above: *Paratrechina vaga*, *Technomyrmex albipes* and *Rhoptromyrmex wroughtonii*). Most attended trophobionts were polyphagous, producing honeydew on host plants from several families (including all common associations with *Oecophylla* ants, although most of their associations with *Sextius 'kurandae'* were found on the two legume lianas *Entada phaseoloides* and *Caesalpinia traceyi* L. Pedley, Blüthgen and Fiedler 2002). Two specialised plant-homopteran interactions were common: First, the understorey shrub *Clerodendrum traceyi* hosted the leaf gall-forming *Aphis clerodendri*, which was attended by *Paratrechina vaga* and *Technomyrmex albipes* (Carver et al. 2003). Second, *Syzygium 'erythrocalyx'* trees hosted a tree hopper species that represented the most important trophobiont of *Anonychomyrma* ants. Compartmentalisation between ants and trophobionts was significant ($T_{\text{obs}} = 262$, $T_{\text{ran}} = 218 \pm 3$, $p < 0.001$; all coccoids pooled). *Oecophylla* trophobioses were restricted to the upper canopy. Honeydew use by *Anonychomyrma* ranged from the basal trunk (e.g. on trunk-borne flowers) towards the upper crown of the relatively small *S. 'erythrocalyx'* trees (< 15 m). All other ant species only attended homopterans on understorey shrubs. The number of ant

Table 5. Associations between honeydew-producing insects, ants, and host plants of trophobionts. Numbers are observations on different plant individuals (climbing plants pooled with their host trees). Host plants are given for trophobiont species found on more than one plant individual ('var. fam.' = various plant families). For full ant and plant names, see Table 1 and 2.

| Trophobionts | | Ants | | | | | | Plants |
|----------------|--|--------------------------|-----------------------|----------------------------|----------------------|-----------------------------|-------------------------|------------------------|
| | | <i>Ano. gilberti</i> | <i>Cre. fusca</i> | <i>Oec. smaragdina</i> | <i>Par. vaga</i> | <i>Rho. wroughtonii</i> | <i>Tec. albipes</i> | |
| COCCIDAE | <i>Coccus hesperidum</i> Linnaeus ¹⁾ | – | – | 6 | – | – | – | var. fam. |
| | <i>Milviscutotulus mangiferae</i> (Green) | 1 | – | 9 | – | 2 | – | var. fam. |
| DIASPIDIDAE | <i>Pseudaulacaspis</i> sp. | – | – | – | – | 1 | – | – |
| ERIOCOCCIDAE | (Gen. indet.) | – | 1 | 2 | – | – | – | var. fam. |
| MARGARODIDAE | <i>Icerya</i> sp. | 1 | – | 1 | – | – | – | var. fam. |
| PSEUDOCOCCIDAE | <i>Planococcus citri</i> Risso | – | – | 1 | – | – | – | – |
| | <i>Planococcus minor</i> (Maskell) | – | – | 3 | – | – | – | var. fam. |
| COCCOIDEA | total (incl. unidentified) | 2 | 2 | 36 | 1 | 8 | 1 | – |
| APHIDAE | <i>Toxoptera aurantii</i> (Boyer de Fonscolombe) | 1 | 1 | 4 | – | 3 | – | var. fam. |
| | <i>Aphis clerodendri</i> Matsumura | – | – | – | 5 | – | 8 | <i>C. tracyanum</i> |
| | <i>Austrotartessus</i> spp. | – | – | 2 | – | – | – | <i>C. sublimis</i> |
| | Idiocerinae: Gen. nov. | 6 | – | – | – | – | – | <i>S. erythrocalyx</i> |
| MEMBRACIDAE | <i>Sextius kurandae</i> | – | – | 22 | – | – | – | var. fam. |
| LYCAENIDAE | <i>Anthene seltutius</i> (Röber) | – | – | 1 | – | – | – | – |
| | <i>Arhopala centaurus</i> group | – | – | 1 | – | – | – | – |

¹⁾ including samples that could only be identified to genus level.

individuals foraging on honeydew was systematically examined only for *Oecophylla* (median 449 ants per tree crown, range: 20–1218, $n = 26$ surveys from 11 trees, Blüthgen and Fiedler 2002). Values for *Anonychomyrma* on *S. 'erythrocalyx'* may be similar or higher (true counts were impossible in the dense foliage of these trees, and ants and cicadellids were too mobile). The median number of *Oecophylla* vs *Anonychomyrma* workers per plant that forage simultaneously for extrafloral or floral nectar was three vs five, respectively. Thus for any colony of the dominant ant species, the number of workers collecting honeydew may be typically 10–100 times as high as those nectar collecting. Trophobiotic associations of the other species included only 1–35 ant individuals per plant, but higher values for ants within leaf galls of *C. traceyi* (up to a few hundred individuals where ant nests were found inside the galls).

Co-occurrence and species replacement

Co-occurrence ($S > 1$) and replacement ($R_s > 0$) of ant species on plants were significantly more common on nectar (EFNs and FNs) than on honeydew sources, where no case of co-occurrence and no replacement of ant species was observed (Table 6). Furthermore, co-occurrences varied substantially between plant species with EFNs or FNs (Fig. 1a). On three plant species, co-occurrences were found in all surveys with more than one ant worker present, while the lower extreme was represented by *Flagellaria* (13%) and *Smilax* (0%). Four of these cases deviated significantly from the expected proportion (33%) for all plants (Fig. 1a); the proportion

of all surveys (including those with a single ant worker) was 23%. Variation among ant species was similar (Fig. 1b), ranging from 9% to 100% (total for all ant species: 46%). The two dominant ants and those ant species that were rarely observed together with the dominants (above category 4) infrequently co-occurred with any other ant on nectar plants. In turn, co-occurrences represent large proportions of the visits for several sub-ordinate ant species typically found in territories of the dominants, significantly higher than expected in four species (Fig. 1b). There was a weak positive relationship between co-occurrence frequency and plant attractiveness expressed as the mean number of ant individuals per plant species (Spearman's $r_s = 0.43$; $p = 0.04$; $n = 23$ plant species), and a positive correlation between the number of ant species and individuals per survey ($r_s = 0.25$; $p < 0.001$; $n = 391$ surveys with at least two ant workers).

Discussion

Most ants are at least partly carnivorous or scavengers (Stradling 1978), but honeydew and nectar represent key resources for arboreal ant species (Tobin 1995, Davidson 1997, Davidson et al. 2003) and are obviously more predictable than prey (Jackson 1984b, Yanoviak and Kaspari 2000). The importance of honeydew and nectar could be confirmed by their strong bottom-up effects on the ant community structure in our study, and is also corroborated by results from stable isotope analysis (Blüthgen et al. 2003). Differences between honeydew and nectar utilization were pronounced at our Austra-

Table 6. Frequency of co-occurrence and replacement of ant species foraging on extrafloral nectaries (EFNs), floral nectaries (FNs), or honeydew sources (per plant individual). n_1 = number of records per plant during all surveys (only those surveys with at least two ant individuals), n_2 = number of comparisons between consecutive surveys (negative records excluded). Different letters in χ^2 column indicate significant differences between resources in frequency of ant co-occurrence or replacement, respectively (χ^2 -test on absolute frequencies between all three pairwise resource combinations, Bonferroni corrected, $df = 2$).

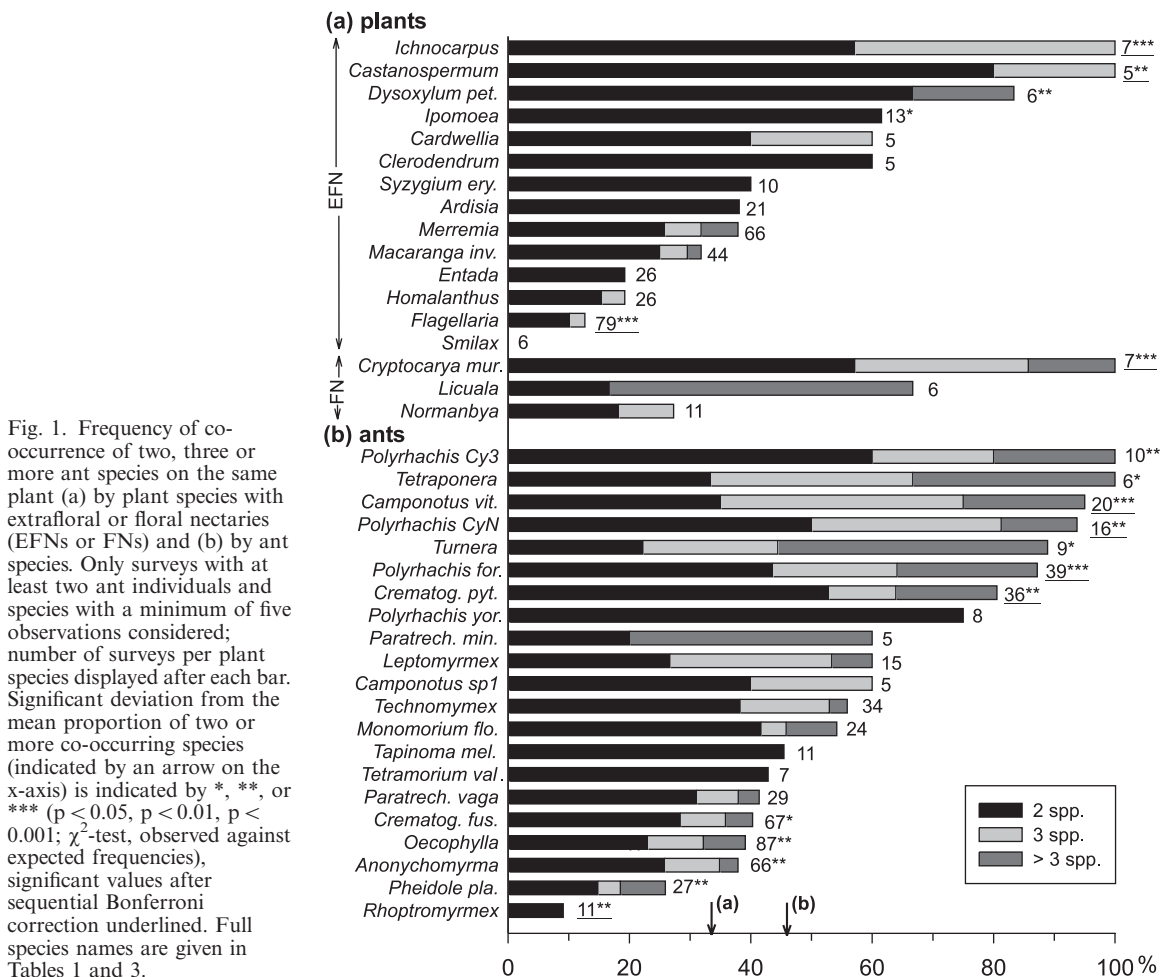
| Resource | Ant species co-occurrence | | | | | Ant species replacement | | | | |
|----------|---------------------------|--------|--------|----------|----------|-------------------------|-----------|---------------|-----------|----------|
| | n_1 | 1 sp. | 2 spp. | > 2 spp. | χ^2 | n_2 | $R_s = 0$ | $0 < R_s < 1$ | $R_s = 1$ | χ^2 |
| EFNs | 360 | 68.1% | 24.2% | 7.8% | a | 103 | 49.5% | 1.0% | 49.5% | a |
| FNs | 42 | 54.8% | 28.6% | 16.7% | a | 9 | 55.6% | 11.1% | 33.3% | a |
| Honeydew | 81 | 100.0% | 0.0% | 0.0% | b | 22 | 100.0% | 0.0% | 0.0% | b |

lian study site, and this comparison provided some general insights into structuring mechanisms for the ant community.

- 1) Nectaries were usually visited by a dynamic and opportunistic ant assemblage, similar to other nectar ant communities reported elsewhere (Schemske 1982, Oliveira and Brandão 1991,

Blüthgen et al. 2000b). Non-aggressive co-occurrence of different ant species was common, and assemblages on individual plants were temporally variable. Ant species strongly overlapped in their choices of plant species visited for nectar, although overall species partitioning was significant.

- 2) The ant community on honeydew sources was substantially different: co-occurrence was comple-



tely lacking as well as species replacement. While nectaries were visited by a broad spectrum of ants, use of honeydew sources was limited to a small subset of these species. Trophobiont species partitioning was pronounced, particularly between the two dominant ant species. In effect, most honeydew sources were monopolised by a colony of one of the two dominant ant species, particularly in the canopy (Blüthgen and Fiedler 2002), or by a colony representing one of four ant species in the understorey. Reduced diversity and higher territoriality of trophobiotic ants appear to be more or less ubiquitous as previously found in other ecosystems (Brian 1955, Dejean et al. 1997, Blüthgen et al. 2000b).

The distinct compartmentalisation of honeydew and nectar sources may result in a cascade of effects, visualised in Fig. 2. Beyond these effects, consequences for the distribution of other arthropods and plant herbivory can be expected (Horvitz and Schemske 1984). Our results provide evidence that the distribution of plants that are hosts for a few key homopteran species shapes the distribution of dominant ants, with legume lianas (Blüthgen and Fiedler 2002) and *Syzygium 'erythrocalyx'* trees as keystone species in the study area. Besides providing nectar and hosting trophobionts, the latter tree species is primarily important in providing

nest sites – all *Anonychomyrma gilberti* colonies in the study site lived in the hollow trunks of this common tree (Monteith 1986; some were inhabited by *Crematogaster* cf. *fusca*, N. Blüthgen, unpubl.). The assemblage of hierarchically inferior ant species may consequently be determined by the distribution of the dominants. This asymmetrical competition may hold responsible for the observed segregation in plant species associations: ant species that were commonly tolerated by the dominants were significantly different in their nectar plant choices from those ant species that rarely co-occurred with the dominants (Table 4). The latter group includes three species that monopolised large aggregations of homopterans on understorey shrubs, rendering them sub-dominant ants in a relatively specialised niche. Besides these specific trophobioses, opportunistic foraging on nectar may be crucial for all non-dominant ants, since most EFNs and FNs were not monopolised or fully exploited by the dominant species. Moreover, many EFNs occur on understorey plants on which dominant ants were less active. Overall, the patterns of co-occurrence versus resource monopolisation found in our study provide strong support for the importance of asymmetric interspecific competition in the structuring of ant communities demonstrated previously in various experimental (Fellers 1987, Savolainen and Vepsäläinen 1988, Andersen 1992, Perfecto 1994) and ant mosaic studies (Room 1971, 1975, Taylor and Adedoyin

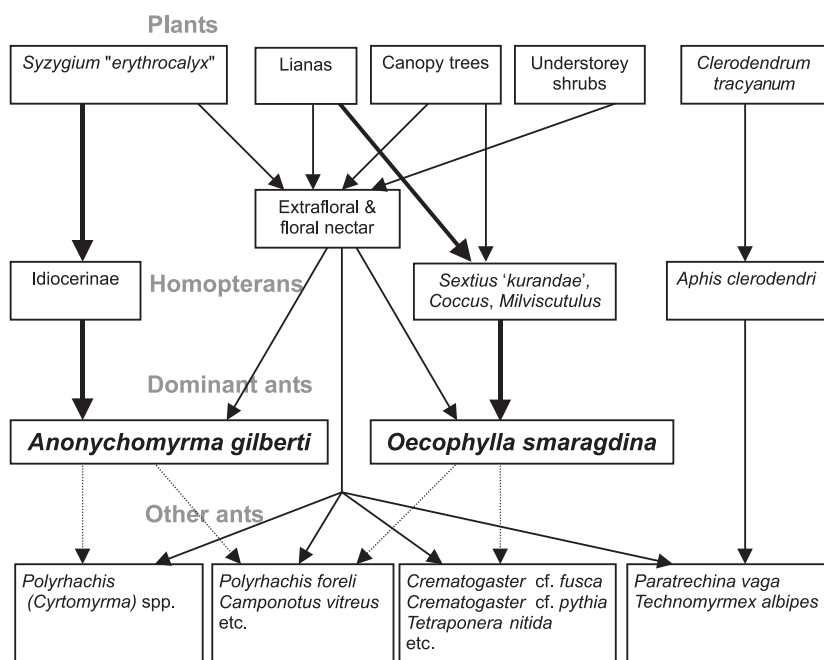


Fig. 2. Model visualising the main elements of the investigated multitrophic food web and proposed, simplified effects on community composition in the arboreal ant community in tropical rainforest in North Queensland, Australia. Continuous lines: resource links (bottom-up effects), dotted lines: common co-occurrences between ant species.

1978, Jackson 1984a, Majer 1993). This asymmetry is associated with variation in the relative importance of co-occurrences across the dominance hierarchy: the two dominant ants are common and often shared nectar sources with their subordinate species, but the proportion of such co-occurrences is relatively low. In turn, for many of the subordinate ants, co-occurrences are much more frequent and may include most of their plant visits. Thus, the ant mosaic in this study is based on a mixture of specialised processes nested in the bottom-up control by plants, and horizontal effects of ant competition on generalised resources.

Co-occurrence and specialisation are two features that may or may not be linked, hence putative underlying mechanisms are discussed separately.

Co-occurrence

Several factors may promote or inhibit coexistence of ant species on the same resources:

- 1) the architecture of plants may facilitate defence which can be efficiently concentrated on basal structures (Hölldobler and Lumsden 1980, Jackson 1984b; myrmecophytes: Davidson and McKey 1993). Spatial structure may be important here, since most honeydew and certain nectar sources are spatially more concentrated than nectaries that are often scattered over the entire plant.
- 2) Temporal niche differentiation may allow for coexistence of competitors, e.g. a turnover between diurnal and nocturnal ant assemblages (Albrecht and Gotelli 2001, Hossaert-McKey et al. 2001), although dial partitioning (albeit significant) was not very strong in the community studied where most ants were more or less continuously active.
- 3) Interspecific differences in the speed of resource discovery may be important permitting several species to exploit the same resources, implying a trade-off between (early) discovery and (later) dominance of a food source (Davidson 1998). Such successional patterns have been demonstrated for ants at baits (Fellers 1987, Perfecto 1994). Temporal patterns of nectar and honeydew secretion may vary, so that restricted productivity (ephemeral sources) may maintain a higher ant species diversity, while more continuously supplied resources (particularly honeydew) are monopolised by the few dominant ants in the long run.
- 4) Benefits from resource monopolisation should increase with the predictability of a source. Tropical litter ant communities may be very unstable and there is little evidence of interspecific competition for food (mostly prey, Kaspari 1996, Yanoviak and Kaspari 2000) or exclusive territories (Jackson

1984b). Honeydew is certainly one of the most predictable and stable resources, and moreover it can be largely controlled by the ants themselves.

- 5) Food quantity and quality may have a key role in the partitioning of ant attendance. Honeydew is a relatively nutritious and rewarding resource, its major nutrients are a wide spectrum of carbohydrates (mono-, di- and trisaccharides) and amino acids (Douglas 1993, Völkl et al. 1999). Nectar composition is often more limited, both in regard to sugars (often only containing sucrose and its components glucose and fructose) and amino acids, although variability between plants is high (Percival 1961, Baker et al. 1978).

If nectar indeed represents a poorer resource than honeydew, monopolisation should be less economical. Nevertheless, more gradual variability between nectar sources may reveal independent information about a correlation between resource quality and visitation. Some plants, such as *Flagellaria* and *Smilax*, continuously offer large amounts of nectar and attracted many ants. These were often from one of the two dominant ants that defended the plant against competitors (Fig. 1). Nectar from these two species is characterised by a high concentration and a broad spectrum of amino acids, similar to honeydew (Blüthgen and Fiedler 2004a, Blüthgen et al. 2004). Such mixtures of amino acids are highly attractive to ants (Blüthgen and Fiedler 2004b). In contrast, typical nectar plants were not monopolised, even where high numbers of ants had been attracted (there was a positive relationship between number of ant individuals and species).

Specialisation

Trophobiotic interactions at our study site are much more specialised than interactions involving nectar, despite the fact that all honeydew-feeding ants were opportunistic and among the most common nectar feeders. On a continuum between facultative and obligate interactions, EFN-mediated interactions are probably far more facultative for ants and plants than many trophobioses. Homopterans often depend on this mutualism, which may drive specialisation processes, but most trophobiotic systems are less specific and more opportunistic (Stadler and Dixon 1998). In the present study, non-trophobiotic ants may have either been effectively excluded from honeydew by aggressive defence, or they were otherwise not capable of trophobiotic interactions or may have different resource requirements. However, the large overlap in nectar harvested by trophobiotic and non-trophobiotic ants, plus their numerical and behavioural dominance on nectaries, supports the view that competitive exclusion is at act (Blüthgen and Fiedler 2004a). The species-specificity within the trophobiotic

community is not driven by the trophobiotic potential of the ants, either. When *Sextius 'kurandae'* aggregations were transferred from *Oecophylla* colonies to *Anonychomyrma*, they were readily accepted by their new ant partner and attended for honeydew for over five days (N. Blüthgen, unpubl.), although other more obligate trophobioses may not allow for ant interchange (lycaenids: Fiedler et al. 1996, Seufert and Fiedler 1996).

The degree of specificity varies between different animal-plant systems. Pollination systems are usually very generalised at the community level (Waser et al. 1996) in both tropical and non-tropical ecosystems (Ollerton and Cranmer 2002). Some tropical herbivore communities may also have low degrees of specialisation (Novotny et al. 2002), while others may be quite specialised in both tropical and temperate environments (Fiedler 1998). Frugivores may be similarly generalistic (Fuentes 1995). In contrast, myrmecophytism (plants with ant-inhabited domatia) often involves a high degree of specialisation in the ant community (Fonseca and Ganade 1996), although in non-specialised structures such as tank bromeliads, ant communities are randomly organised (Blüthgen et al. 2000a). Among ant-tended butterfly larvae there is a gradient from broad opportunism in facultative associations towards high specialisation in obligate interactions with dominant ants (Fiedler 2001). Placing the differential visitation pattern of honeydew and nectar into this context, it seems that high-quality resources, where interspecific competition is pronounced, could be more prone to specificity between partners, probably via monopolisation by dominant members of the community, and may promote specialisation.

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