How availability and quality of nectar and honeydew shape an Australian rainforest ant community

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'Go to the ant, thou sluggard;
consider her ways and be wise'
<Proverbs 6: 6>

Meinen Eltern gewidmet

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Introduction

Biodiversity

Studies about biodiversity are of growing importance both for basic biological disciplines such as ecology and evolutionary biology as well as for applied conservation issues including ecosystem monitoring and management strategies (Wilson 1988, Lovejoy 1994). The question whether biodiversity is important for ecosystem functioning and stability attracts much attention in the scientific community. Recent theoretical work predicted positive relationships between diversity and stability (McCann et al. 1998, Polis 1998, McCann 2000, but see May 1973). Empirical studies detected positive correlations between biodiversity and ecosystem functions such as net primary productivity (Hector et al. 1999), resistance against invasions (Naeem et al. 2000), or buffering functions against density fluctuations or environmental stress (Tilman & Downing 1994, Naeem & Li 1997) among multiple other factors (Schulze & Mooney 1993). Such recent empirical progress was largely based on controlled experiments with isolated microcosms or relatively simple modified ecosystems (Lawton 1994, 1995, 1996, Naeem et al. 1994, Tilman & Downing 1994, McGrady-Steed et al. 1997, Naeem & Li 1997, Tilman et al. 1997, Hector et al. 1999, Hulot et al. 2000, Bradford et al. 2002). However, methods and conclusions of these studies have been subject to vehement critique and were controversially debated in leading scientific journals (Huston 1997, Wardle 1998, Huston et al. 2000, Loreau & Hector 2001). We are still only beginning to understand fundamental processes associated with species coexistence in diverse multispecies communities. Experiments in complex natural environments are still strongly limited, despite their unequivocal importance to evaluate the impact of various factors at act. In biodiversity experiments applied to realistic natural scenarios, treatment effects are often difficult to be separated from covariation with uncontrolled parameters, so that conclusions about causality may be problematic (Huston 1997). Consequently, insights into *processes* and mechanisms underlying biodiversity in natural communities often rely on indirect inference gained by analyses of *patterns*.

Both theoretical and empirical work discussed correlations between biodiversity and biogeographical factors and their evolutionary or ecological history, and stressed relationships with various spatial or temporal scales (MacArthur & Wilson 1967, Connor 1986, Colwell & Lees 2000, Partel 2002). Different authors emphasised the importance of habitat heterogeneity, biological interactions, niche partitioning, disturbance regimes,

dispersal limitation, stochastic effects or other factors, in order to explain actual maintenance of diversity among plant or animal assemblages (Connell 1978, Brokaw & Busing 2000, Chesson 2000, Hubbell 2001, Stachowicz 2001, Sheil & Burslem 2003). Across different trophic levels, two levels of mechanisms have been distinguished which may act upon communities: resource-based effects on higher tropic levels (*bottom-up control*) or inverse effects resulting from higher trophic levels, e.g. by predators and parasitoids (*top-down control*). The relative importance of both types of effects is still subject to controversial debates and there is increasing evidence that it may vary between different ecological systems (Hunter & Price 1992, Powers 1992, Polis et al. 2000).

Tropical ecosystems provide a particularly prominent challenge to our understanding about mechanisms generating and maintaining biodiversity, since local communities can be extraordinarily species-rich. Yet, our current knowledge about ecosystems still seems inversely related to their complexity. Comprehensive studies of mere patterns of tropical diversity are progressing intensively only in recent times (e.g. Lawton et al. 1998, Novotny et al. 2002, Pitman et al. 2002, Kaspari et al. 2003; recent doctoral theses of colleagues in Bayreuth: Brehm 2002, Süßenbach 2003), and very few tropical communities have been studied to an extent enabling conclusions about the spatiotemporal dynamics and general processes beyond these patterns (Reagan & Waide 1996, Hubbell et al. 1999, Molino & Sabatier 2001).

The goal of this thesis was to examine *causal* relationships between the availability and quality of resources and the complex community structure of their consumers (bottom-up control and competition) in a tropical rainforest. A resource-based approach was used in an attempt to cover a representative spectrum of liquid resources – nectar and honeydew – and their main consumers – ants – from a single defined rainforest habitat. Analyses of community patterns were supplemented by controlled experiments in order to establish causal links between resource traits and differential resource use. Hence this study attempted to combine analyses of patterns and processes.

Nectar and honeydew

Nectar-mediated interactions involve a broad assemblage of producing plants and consuming animals. Nectar serves as one of the pollinator attractants in the majority of flowers, and the mutualistic role of nectarivores in flower pollination has been widely documented (Faegri & van der Pijl 1979, Bentley & Elias 1983), although negative effects of 'nectar-robbing' may interact with flower–pollinator mutualism (Galen 1983, Inouye

1983, Irwin & Brody 1998). Studies on flower partitioning in nectarivore communities have been usually based on observed encounters and resulting species interaction matrices (Waser et al. 1996, Ollerton & Cranmer 2002). However, the mechanistic chemical basis for these relationships remains largely unknown, since documented patterns of nectarivore communities have usually not been linked to nectar quality measures. Some studies broadly attempted to correlate nectar composition with flower visitor taxa across different habitats (Percival 1961, Baker & Baker 1973, Baker & Baker 1983), but their 'characteristic' visitor spectrum has not been quantified, and uncontrolled floral traits (e.g. pollen, shape, colour, odour) may interact with nectar composition. On the other hand, preferences for nectar characteristics have been examined in detail for a growing number of nectarivore species (e.g. Lanza 1991, Rusterholz & Erhardt 1997, Wäckers 1999, Blem et al. 2000), but usually under isolated and controlled conditions rather than in their natural environment. To date, little effort has been made to upscale such idiosyncratic or species-specific physiological preferences to more natural situations in multispecies communities.

Besides floral nectar, extrafloral nectaries (EFNs) are particularly common in tropical regions, often occurring on great proportions of plant species and individuals from a given habitat (Oliveira & Oliveira-Filho 1991, Fiala & Linsenmair 1995, Pemberton 1998, Blüthgen et al. 2000b). The main visitors of EFNs are ants, which was unequivocally noted in most studies (Bentley 1977, Koptur 1992) although not universally (Hespenheide 1985). Ants attracted to EFNs have been often documented to benefit plants in terms of herbivore protection (Inouye & Taylor 1979, Koptur 1979, Stephenson 1982, Oliveira 1997), although not all interactions proved to be mutually beneficial (O'Dowd & Catchpole 1983, Heads & Lawton 1985, Whalen & Mackay 1988). Unlike flower–visitor community studies, most investigations on nectarivore assemblages on EFNs have focused on single or few plant species from each habitat, thus little information is available on potential resource partitioning, the degree of ant–EFN specialisation and the importance of nectar composition. This differs from interactions between ants and plant domatia (myrmecophytism) where many community studies are available (Davidson & McKey 1993, Fonseca & Ganade 1996, Yu & Davidson 1997, Blüthgen et al. 2000a).

Unlike EFNs, flower nectars are less commonly used by ants (Janzen 1977). Several cases have been noted where either floral nectars (Feinsinger & Swarm 1978) or floral tissues (Willmer & Stone 1997, Ghazoul 2001) were repellent against ants, although the overall importance of these ant-repellent functions in flowers has been questioned (Haber et al. 1981, Koptur & Truong 1998). Pollination services by ants are usually very limited for

several reasons including reduced pollen viability due to glandular secretions on the ant's body (Beattie et al. 1985), and only few cases of obligate ant-pollination have been found (Peakall et al. 1991, Gómez et al. 1996). Instead, ants often function as floral nectar thieves and negatively affect plant fitness (Galen 1983, Willmer & Stone 1997).

One major source of liquid food for many ant species is honeydew, i.e. excretions from herbivorous insects. In many cases, ants and herbivores maintain close associations known as trophobioses. Trophobiotic partners of ants include homopterans (Hemiptera: Auchenorrhyncha and Sternorrhyncha), caterpillars (Lepidoptera: Lycaenidae and Riodinidae) and occasionally heteropterans (Buckley 1987, Hölldobler & Wilson 1990, DeVries 1991a, Fiedler 1995, Gibernau & Dejean 2001). Trophobionts often benefit from ant attendance through their defence of parasites and predators, prevention of honeydew accumulation or other services (Way 1963, Buckley 1990, Bach 1991, Cushman & Whitham 1991). Benefits are variable and conditional (Bristow 1984, Cushman & Whitham 1989, Itioka & Inoue 1996, Del-Claro & Oliveira 2000, Morales 2000, Fischer et al. 2001), and ant-attendance may also involve costs (Stadler & Dixon 1998, Yao et al. 2000). Some trophobioses may thus have neutral or negative net effects for the herbivore (Stadler et al. 2001). Correspondingly, associations range from obligate ant attendance to facultative interactions (Buckley 1987, Fiedler 1991, 1998, Eastwood & Fraser 1999). The degree of specialisation between trophobiotic partners may vary, although preferences are usually more pronounced than in nectar-mediated interactions (Bigger 1993, Seufert & Fiedler 1996). Large colonies of dominant ants in temperate and tropical ecosystems often maintain extensive trophobioses (Horstmann 1972, Davidson 1997, Blüthgen et al. 2000b, Dejean et al. 2000). Nevertheless, most trophobiotic ant species are omnivores and consume nectar and other liquids as well as prey and other diets (Stradling 1978, DeVries 1991b, Rico-Gray 1993, Fiedler 2001). Nomadic *Dolichoderus* ants in tropical Asia may exclusively feed on honeydew, but this case is highly exceptional (Maschwitz & Hänel 1985).

While many studies examined the effects of trophobioses on herbivore and host plant performance (Messina 1981, Buckley 1983, 1987, Fritz 1983, Floate & Whitham 1994), the chemical background of honeydew and nectar use by ants is less well understood. Carbohydrates are the main component of these resources, but amino acids and various other substances are also common (Auclair 1963, Baker et al. 1978, Baker & Baker 1983, Völkl et al. 1999). Both sugars and amino acids may affect foraging decisions of ants (Lanza & Krauss 1984, Lanza et al. 1993, Koptur & Truong 1998, Völkl et al. 1999, Tinti

& Nofre 2001, Wada et al. 2001), but their relative importance for preferences and resource selection in complex ant communities has not been examined thus far.

Ant communities

The dominant and influential role of ants in tropical ecosystems has been recognised for a long time in the scientific literature (Schimper 1888, Bequaert 1922). Quantitative surveys confirmed that ants are among the most abundant animals in many tropical habitats (Fittkau & Klinge 1973, Hölldobler & Wilson 1990, Stork 1991, Floren & Linsenmair 1997). It is therefore surprising that questions about resources and other factors that drive the ants' community structure have only just recently started to get attention.

Many studies emphasised the role of ants as predators. Ant predation has been demonstrated to affect the composition of arthropod communities in temperate (Skinner & Whittaker 1981, Karhu 1998) and tropical forests (Floren et al. 2002), or in plantations where ants have important functions as biological control agents (Majer 1976a, Way & Khoo 1992). Such effects are most prominent in invasive ant species that may have severe impacts on the native local fauna (Holway 1998, Hoffmann et al. 1999).

However, the superabundance of ants in tropical forest canopies (Stork 1991, Floren & Linsenmair 1997) has led to the prediction that they should obtain large proportions of their diet through nectar and honeydew, thus canopy ants should occupy very basic trophic positions (Tobin 1991, 1994, 1995, Davidson & Patrell-Kim 1996). Dominant canopy ants have been shown to possess characteristics that facilitate their liquid food storage (proventriculus) or increase their capability to live on nitrogen-poor plant diets (Davidson 1997). Indirect support to the nitrogen limitation of canopy ants came from experiments using sugar-based and protein-based baits (Yanoviak & Kaspari 2000). However, nutrient fluxes and trophic positions are difficult to test for omnivorous ants, and although recent observations in rainforest canopies have shown the great extent of plant exudate feeding in many ant species (Blüthgen et al. 2000b, Dejean et al. 2000), the relative importance of different diets has rarely been quantified except for true plant-ants on myrmecophytes (Sagers et al. 2000, Fischer et al. 2002).

Local ant communities can be very species-rich (Wilson 1959, Longino & Colwell 1997, Brühl et al. 1999), although they often constitute only a relatively small fraction of the diversity of some other insect taxa (Stork 1991, Floren & Linsenmair 1997). Diversity patterns of tropical ant faunas have been studied extensively in various habitats and along different gradients (Longino & Nadkarni 1990, Kaspari 1996, Brühl et al. 1998, 1999,

Feener & Schupp 1998, Majer et al. 2001, Kaspari et al. 2003). Interspecific competition between ants is usually pronounced (Jackson 1984a), and some species establish territories that are aggressively defended against other species (Hölldobler & Lumsden 1980, Hölldobler 1983). In effect, hierarchically dominant ants were found to maintain mutually exclusive territories, in which only a specific subset of the ant fauna is tolerated (Room 1971, Hölldobler 1983, Mercier et al. 1998). Such territorial distribution patterns have been termed 'ant mosaics' and were originally described from structurally simple plantations (Room 1971, 1975, Majer 1972, 1993, Taylor 1977, Jackson 1984b) and secondary forests (Leston 1978), before they have been detected in mangroves (Adams 1994a) and rainforests (Dejean et al. 2000, Dejean & Corbara 2003). However, the structural role of competition in ant species distributions and their importance in rainforest communities are not universally accepted (Floren & Linsenmair 2000, Ribas & Schoereder 2002).

Outline

This thesis aims to link community patterns with ecological and physiological processes based on preferences of individual component species and their interactions in the community. At the beginning, bottom-up effects of plant-based resources (nectar, wound sap) or trophobiotic herbivores (honeydew) on nectar feeding ant communities were analysed. This includes a detailed description of extrafloral nectaries used by ants (*Chapter 1*), an analysis of ant communities attending nectar and honeydew sources (*Chapter 2*) and of the resource quality with respect to sugar and amino acid composition (*Chapter 3*), as well as a characterisation of some of the trophobiotic interactions involved in honeydew consumption (*Chapter 4+5*). Preferences for sugar and amino acid mixtures were investigated experimentally with artificial solutions (*Chapter 6*). Finally, the nutrient flow from nectar or honeydew diets was compared between ant species and colonies using stable isotope analysis (*Chapter 7*).

Chapter 1 – Structure and distribution of extrafloral nectaries

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Abstract

Extrafloral nectaries (EFNs) are of ecological, evolutionary, and taxonomic importance in many plants, but are often overlooked in botanical descriptions and have thus far not been studied in humid Australian forests. We examined EFNs in a tropical rainforest in North Queensland, Australia. A total of 29 plant species were found bearing EFNs within the 1 ha study plot at the Australian Canopy Crane Project, and an additional 10 EFN species were found in rainforests and other habitats outside, but nearby the plot. The records include 12 genera in which EFNs have not been previously reported (*Ardisia, Bambusa, Castanospermum, Dysoxylum, Melicope, Flagellaria, Glochidion, Ichnocarpus, Merremia, Rockinghamia, Syzygium, Wrightia*) including one new family (Flagellariaceae). In the study plot, 13 tree species (17% of tree species with dbh > 10 cm), 10 climbing plant species (21%), and six shrubs had EFNs, a similar proportion compared to tropical forests on other continents. Morphology of most EFNs was studied using scanning electron and light microscopy. EFNs were assigned to five different structural types (*sensu* Zimmermann 1932): flattened, elevated, pit, scale-like, and formless nectaries. EFNs from all species were regularly visited by ants, allowing detection of many otherwise inconspicuous nectaries.

Introduction

Extrafloral nectaries (EFNs hereafter) have been described from well over 300 plant genera and more than 90 plant families (Zimmermann 1932, Elias 1983, Koptur 1992). More recent field surveys have further considerably increased the list of plant taxa bearing EFNs (e.g. Fiala & Linsenmair 1995, Pemberton 1998). The frequency of EFN-plants in local floras is high in the tropics, e.g. 32% of woody plant species in a study in Panama (Schupp & Feener 1991) or 12% in a Malaysian forest (Fiala & Linsenmair 1995).

The Australian floral region has been of considerable interest in terms of evolutionary history, including the relatively isolated rainforest patches in northern Queensland (Webb & Tracey 1981, Adams 1994b). However, there are no surveys of EFN-plants nor any ecological or morphological studies of EFNs from Australian rainforests. Investigations on EFNs in Australia have been largely restricted to plants from more arid regions, namely acacias (Marginson et al. 1985, Knox et al. 1986, Knox et al. 1987), *Adriana* (Euphorbiaceae) (MacKay & Whalen 1998) and *Chamelaucium uncinatum* (Mytraceae) (O'Brien 1995). A list of 13 EFN-bearing plant species in arid South-West Australia was compiled by Lamont (1979).

EFNs have evolved independently many times and are highly variable in their morphological and anatomical structure, although seven morphological types can be recognised (Zimmermann 1932, Elias 1983). The ecological function of EFNs has been subject to controversial debates in the past (see Bentley 1977). However, evidence for the 'protectionist' hypothesis, i.e. attraction of beneficial insects, now seems compelling and is widely accepted (Bentley 1977, Koptur 1992), although this function may not apply to all EFN-plants. The main visitors of most EFNs are undoubtedly ants, and the secreted nectar provides an important resource for a wide spectrum of largely omnivorous ant species (Blüthgen et al. 2000b). In general, the high abundance of ants in rainforest canopies may be largely dependent on nectar and honeydew (Davidson 1997), which was also typical for the study site (*Chapter 5*). Protective effects of ants conferred to EFN plants include a reduced presence of herbivores and seed predators (Tilman 1978, Smiley 1986), and this often translates into parameters of plant fitness such as decreased herbivory level (Stephenson 1982, Koptur et al. 1998), increased plant growth and survival (Buckley 1983, Kelly 1986) and higher fruit set (Koptur 1979, Oliveira 1997).

The objectives of this study were (1) to fill a prominent biogeographic and taxonomic gap in the knowledge of EFNs in the Australian rainforest, (2) to measure the relative abundance of EFN-plants in different life-forms and forest stages, and (3) to provide a brief morphological and anatomical characterisation and comparison of some of the EFNs in order to stimulate more detailed studies on the functional anatomy of the most interesting cases in the future.

Material and Methods

The study was conducted at the Australian Canopy Crane Facility in Cape Tribulation (North Queensland, Australia; 16°07' S, 145°27' E, 80 m a.s.l.). The site is located in a lowland area between the coastline and a

mountain range and comprises complex mesophyll vine forest (Tracey 1982) with an average canopy height of ca. 25 m. The local climate is very wet with a strong seasonality. Average rainfall amounts to ca. 3500 mm per year, of which about 60% occur in the wet season between December and March. Mean daily temperature ranges between 22°C (July) and 28°C (January) (Turton et al. 1999). After the canopy crane was installed by helicopter in a mature forest patch in November 1998, the forest suffered severe damage by cyclone 'Rona' in February 1999. Since then, a rapid recovery of the forest has been noted. As a consequence of the cyclone disturbance, the forest comprised patches of relatively open and closed canopy during the study time (January–August 2001). The canopy crane is 48.5 m tall with a jib length of 55 m, allowing researchers to study the canopy in a forest area of over 0.95 ha. Unless stated otherwise, results from this study relate to this area covered by the jib, henceforth denoted as the 'crane site', and its immediate surrounding forest. Many EFNs caught our attention through visual inspections of ant activity on plants, especially on young plant tissue. Locations of nectaries and the presence of sugars were then confirmed with glucose indicator paper (Glucotix, Bayer), most of them additionally with a handheld refractometer (Eclipse, Bellingham & Stanley Ltd) and HPLC (results not shown). Thus all taxa with EFNs reported in this study proved (1) to attract ants and (2) to secrete a sugar solution. Nectar quantity was measured using 1 µl or 10 µl microcapillary tubes after excluding ants from nectary access overnight using resinous glue (Tanglefoot) on plant stems.

The proportion of tree species and individuals bearing EFNs was calculated on the basis of a survey of 575 trees (dbh over 10 cm; excluding palms, unidentified trees and dead trees) conducted in 2001 at the crane site (A. Small, pers. comm.). Species of climbing plants (restricted to angiosperms, including root climbers) were recorded within the crane site by the authors and checked for the presence of EFNs, but a complete survey was not intended. In order to measure the relative abundance of EFN-bearing climbing plants and shrubs, we randomly selected 10 plots of 5 × 5 m area within the crane site (large canopy openings, estimated canopy cover 40–70%), and 10 equally sized plots in relatively mature forest patches all within 500 m radius of the crane site (relatively closed canopy cover 70–90%). Stems of all plants with an obvious climbing habit occurring in the plots at 1.5 m above ground were counted, including multiple stems from single individuals. These were assigned to one of the 12 climbing plant species known to have EFNs (Table 1) or a pooled group of remaining species (assumed to lack EFNs). All self-supporting plants (> 1.5 m height, dbh < 5 cm, rooting in the plot) were counted as 'shrubs'. The relative proportion of individuals and species bearing EFNs was calculated as per cent of total number of individuals and species of the respective life-form recorded in the crane site or the subplots, respectively.

For the description of EFNs in the field, we noted the plant structures involved, the activity of nectar secretion (either as visible nectar droplets or as ant visitation) on different parts of the plant or plant sizes, during day- and night-time, and different seasons, and the visitation by ants and other arthropods.

Plant material was collected in 70% ethanol for scanning electron microscopy (SEM; LEO 440i, Leo Electron Microscopy Ltd., Cambridge, UK). Samples were sequentially transferred into 100% ethanol, critical-point dried and coated with gold-palladium. Studies using light microscopy (LM) were carried out on freshly collected material using razor blade sections. It was not the intention to provide comprehensive morphological and anatomical descriptions of particular EFNs, as have been undertaken for a small number of species in other studies. Our goal was to provide an overview of the structural variation found within a wide taxonomic range of species as a basis for more detailed studies.

Results

Distribution and abundance

In the rainforest, we found 34 plant species bearing EFNs (Table 1), 29 of which were present within the 1 ha crane site. Five additional species of EFN-plants were found outside the rainforest: *Ipomoea pes-caprae* (L.) R.Br. (Convolvulaceae) and *Hibiscus tiliaceus* L. (Malvaceae) were common at the nearby beaches, while *Acacia* sp. (Fabaceae), *Syzygium pseudofastigiatum* B. Hyland (Myrtaceae), and *Urena lobata* L. (Malvaceae) occurred in other open habitats. Overall, the highest number of species were recorded for Euphorbiaceae (10 species), Fabaceae *s.l.* (6 species), Convolvulaceae and Myrtaceae (3 species each). Eleven EFN-bearing species in the rainforest (34% of all 32 native EFN-bearing species) were endemic to tropical Queensland, i.e. Cape York Peninsula and coastal North-East Queensland (Table 1), including one endemic genus (*Rockinghamia*) (distribution after Jones & Gray 1988, Hyland et al. 1998).

Thirteen tree species had EFNs, constituting 16.9% of the 77 tree species in the crane site and 14.4% of the individual trees (dbh > 10 cm). The most abundant EFN-bearing trees were: *Rockinghamia angustifolia* (6.1%) and *Dysoxylum pettigrewianum* (2.4% of all individual trees). Additional cases representing 'functional' but not 'morphological' EFNs are not considered in the analysis presented here. These include cases where plants were either regularly bitten by ants to induce sap flow (on stems, rachis, and leaflets on many trees of *Cardwellia sublimis* F.Muell., Proteaceae), or where rachillae underneath flowers (especially where flowers or fruits had been aborted) secreted nectar that was readily harvested by ants (*Normanbya normanbyi* (W.Hill) L.H.Bailey, Arecaceae).

The relative abundance of EFN-bearing shrubs (including juvenile trees) in all 20 plots was 12.9%, but there was a strong and significant decrease from the open to the closed forest plots (Figure 1, Mann-Whitney $U = 12.5$, $p < 0.005$, $n = 20$). The total abundance of shrubs (with and without EFNs) remained similar between open (median: 21.5 individuals per plot) and closed forest plots (16.5). The most common shrubs with EFNs were *Homalanthus novoguineensis, Macaranga involucrata* (each in 6 plots, a total of 32 and 12 individuals, respectively), and *Clerodendrum tracyanum* (5 plots, 12 individuals). None of these three species was found in any of the 10 closed forest plots here, where *Ardisia pachyrrhachis* (3 plots, 14 individuals) was the only EFN-bearing species and not found in the open forest, conversely.

Table 1. Plants with extrafloral nectaries in the Australian rainforest (Cape Tribulation, North Queensland). Plant life-forms: climbing plant (cl), herb (he), shrub (sh), and tree (tr). Nectary-bearing plant structures: leaf blades (lf), rachis (rh), petioles (pe), bracts (br), stems (st), between stem and leaf axils (la) or stem and leaf sheaths (sh), inflorescence stems (in), flower peduncles (fp), flower buds (bu), and abaxial surface of calyx (not involved in pollination) (ca). Nectary positions (not applicable in stems): adaxial (ad), abaxial (ab), or structures orthogonal to the axis (o). Morphological nectary types (*sensu* Zimmermann 1932): elevated (E), flattened (F), formless (O), pit (P) and scale-like nectaries (S).

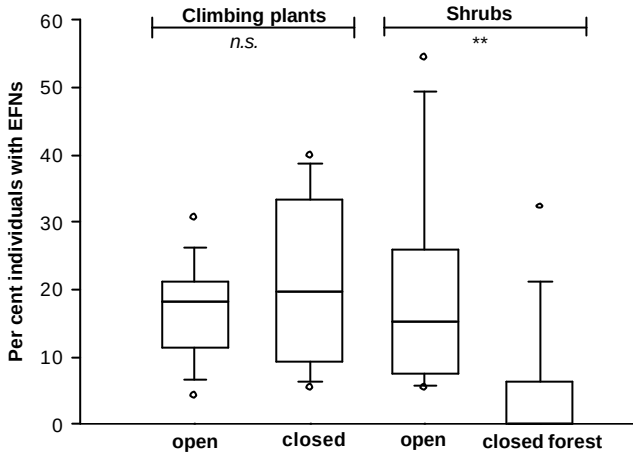
Family	Species	Remarks	Life-form	Structure	Position	Type
Asclepiadaceae	*Wrightia laevis* subsp. *millgar* (Bailey) Ngan	A	tr	ca fp	ab	F
	Ichnocarpus frutescens R.Br.	A	cl	ca	ab	F
Convolvulaceae	*Ipomoea indica* (Burm.) Merr.	C	cl	pe	o	S
	Merremia peltata Merr.	A	cl	pe	ab	S
Cucurbitaceae	*Trichosanthes pentaphylla* F.Muell. ex Benth.	D	cl	br	ab	F
Euphorbiaceae	*Aleurites rockinghamensis* (Baill.) P.I.Forster		sh	pe	ad	E
	Endospermum myrmecophilum L.S.Sm.		tr	pe	ab	E
	Glochidion philippicum (Cav.) C.B.Rob.	A	tr	st fp ca	-	F
	Homalanthus novoguineensis (Warb.) K.Schum.		sh	pe lf	ad ab	F
	Macaranga involucrata subsp. *mallotoides* (F.Muell.) L.M.Perry	E	sh	lf	ad	F
	Macaranga subdentata Benth.	D	tr	lf	ad	F
	Macaranga tanarius Muell. Arg.	B	tr	lf	ad	-
	Mallotus mollissimus (Geiseler) Airy Shaw		sh	lf	ab	F
	Mallotus paniculatus Muell. Arg.	B	tr	lf	ad	F
	Rockinghamia angustifolia (Benth.) Airy Shaw	A D	tr	lf	o	E
Fabaceae	*Archidendron ramiflorum* (F.Muell.) Kosterm.	D	tr	st rh	ad	E
	Castanospermum australe A.Cunn. & Fraser ex Hook	A	tr	st rh	-	F
	Crotalaria sp.	C	he	rh	ad	E
	Entada phaseoloides Merr.		cl	st in	-	P F
	Mucuna gigantea DC.		cl	pe	-	-
Flagellariaceae	*Flagellaria indica* L.	A	cl	sh	-	O
Lamiaceae	*Clerodendrum tracyanum* (F.Muell.) F.Muell. ex Benth.		sh	lf	ab	S
	Faradaya splendida F.Muell.	B D	cl	lf	ab	S
Meliaceae	*Dysoxylum pettigrewianum* F.M.Bailey	A	tr	lf	ad	F
Moraceae	*Ficus septica* Burm. f.		sh	st	-	F
Myrsinaceae	*Ardisia pachyrrhachis* (F.Muell.) F.M.Bailey	A D	sh	lf	ab	S
Myrtaceae	*Syzygium* "*erythrocalyx*" B.Hyland	A D	tr	la	-	-
	Syzygium cormiflorum (F. Muell.) B.Hyland	A D	tr	la	-	-
Passifloraceae	*Adenia heterophylla* (Blume) Koord.	A	cl	lf	ab	F
	Passiflora sp. (Jones and Gray 1988)	D	cl	pe lf	ab	E F
Poaceae	*Bambusa moreheadiana* F.M.Bailey	A B D	cl	sh	-	O
Rosaceae	*Prunus turneriana* (F.M.Bailey) Kalkman		tr	lf	ad	F
Rutaceae	*Melicope elleryana* (F.Muell.) T.G.Hartley	A B	sh	st	-	F
Smilacaceae	*Smilax* cf. *australis*		cl	lf	ab	-

[A] new records of EFNs for the respective plant genus (cf. Koptur 1992; Fiala and Linsenmair 1995)
[B] species not found in the crane site
[C] introduced species
[D] species endemic to North-East Queensland (incl. Cape York Peninsula)
[E] species endemic to Australia

For climbing plants, a higher proportion of EFN-bearing species was recorded than for trees (21.3% of the climbing species found in the crane plot). Their mean abundance in the 25 m^2 plots was also higher (19.1% of the stems). This proportion did not differ significantly between plots with open or closed forest canopy (Figure 1, Mann Whitney

$U = 40$, $p = 0.45$), although there was a pronounced decrease in the absolute number of stems from open (median: 74.5 stems per plot) to closed forest plots (32 stems). The most common species were *Merremia peltata* (16 of the 20 plots, a total of 168 stems), *Entada phaseoloides* (9 plots, 33 stems), and *Flagellaria indica* (6 plots, 20 stems). None of the hemi-epiphytes and root-climbing plants was among the EFN-plants, and no true epiphytes (which were exclusively ferns) with EFNs were found.

Fig. 1. Proportion of plant individuals (climbing plants and shrubs) bearing EFNs in 10 plots (25 m^2) with relative open forest canopy, and 10 plots with relative closed canopy. Boxplots indicating median, quartiles, range and outliers. Differences between open and closed forest plots were not significant (*n.s.*) in climbing plants and highly significant (**: $p < 0.01$) in shrubs (Mann-Whitney U tests, see text).



Nectary activity and visitors

In most EFNs examined in this study, active nectar secretion was usually restricted to young developing tissue (new leaves, inflorescences). Notable exceptions where EFN activity also involved some mature leaves and twigs were *M. peltata* and *E. phaseoloides*. The amount of nectar secretion (measured after ant exclusion from nectaries over night) showed strong variation between species. Among 18 species examined for nectar production, the lowest values of nectar accumulation per leaf (or per stem nectary) were found in *Castanospermum australe*, *D. pettigrewianum*, *F. septica*, *G. philippicum*, *M. elleryana*, *R. angustifolia*, and *T. pentaphylla* (usually < 0.1 µl). Intermediate amounts were found for *A. heterophylla*, *A. pachyrrhachis*, *E. myrmecophilum*, *H. novoguineensis*, *I. indica*, *M. involucrata*, and *Syzygium* '*erythrocalyx*' (0.1–1 µl). The largest nectar quantities were produced by the climbing plants *E. phaseoloides*, *F. indica*, *M. peltata*, and *S.* cf. *australis* (1–10 µl). These nectar accumulations over several hours provide only a rough indication of the high variability between species, since variation between conspecific individuals and between leaves of the same plant was pronounced.

Furthermore, there was a considerable difference between wet months (January–March 2001) and dry months (especially August 2001). In the drier period, EFN activity was negligible in most species, while a few species (*M. involucrata*, *H. novoguineensis*, *F. indica*, and *S.* '*erythrocalyx*') maintained a lower, but persistent activity and ant visitation.

On all plants observed here, ants (Hymenoptera: Formicidae) were obviously the main visitors of EFNs, including 42 species from five subfamilies (Formicinae, Dolichoderinae, Myrmicinae, Ponerinae, and Pseudomyrmecinae). Other regular visitors included (in order of declining frequency): flies (Diptera), jumping spiders (Salticidae, Figure 3c), cockroaches (Blattodea), wasps (Hymenoptera), katydids (Tettigoniidae), beetles (Coleoptera), spring-tails (Collembola), and moths (Lepidoptera). Neither katydids nor spring-tails have been previously reported as EFN-visitors (Koptur 1992), but observations of their nectar foraging were unambiguous and supported by experiments (they were observed feeding on sugar solutions containing sucrose, glucose, and fructose; unpublished data). Visitation patterns and preferences of different ant species for certain EFNs and results of nectar analysis by HPLC will be reported elsewhere.

Nectary morphology

Plant organs bearing EFNs were mostly leaves and leaf petioles, but stems, flower buds, and inflorescence stems were also recorded (Table 1). On all organs except for stems, ad- and ab-axial positions were distinguished (nearest to the adjacent apical internode vs. furthest). Both adaxial and abaxial positions were commonly involved (Table 1) and correspond to the lower vs. upper surface, respectively, of leaves and petioles in all species here.

Five morphological types of nectaries (*sensu* Zimmermann 1932 and Elias 1983) were observed: flattened nectaries (in 12 plant genera found here), elevated nectaries (7), scale-like nectaries (4), formless nectaries (3), and pit nectaries (1). These types were consistent within genera and families with more than one species in this study, except that flattened and elevated nectaries sometimes co-occurred in the same family (Euphorbiaceae, Fabaceae) and even on the same leaf of a plant (*Passiflora* sp.) (Table 1). Structurally these two types are very similar (see below). Furthermore, flattened and pit nectaries co-occur in *E. phaseoloides*. The five morphological types of EFNs correspond to three distinct anatomical arrangements in the species studied:

a) In flattened and elevated nectaries, the epidermis usually forms a cup-like depression in the surrounding mesophyll tissue. On top of this cuboidal epidermis, there are one or a few layers of elongated palisade parenchyma (as a product of periclinal cell division,

also referred to as palisade epidermis) that represent the nectar secreting tissue. A thick cuticle usually covers these nectaries. Nectar release may be through ruptures in the cuticle (see Zimmermann 1932, Durkee 1982), at least in some of the species (see below: *T. pentaphylla*, *Macaranga* spp., *H. novoguineensis*, *D. pettigrewianum*). Pit nectaries are relatively similar.

b) Scale-like nectaries consist of a basal part, a stalk-like structure and a cuboidal head. They are considered as specialised trichomes (protuberances of the epidermis). All parts consist of few or many cells that are not regarded as epidermal parenchyma cells. Without insights into the origin of the tissues, we simply recognise 'stalk tissue' and multicellular nectariferous parenchyma (more or less palisade-like) as 'head tissue' (Zimmermann 1932), also covered by cuticle. As above (a), nectar release may be through ruptures in the cuticle, at least in some cases (*A. pachyrrhachis*, *Faradaya splendida*, see below).

c) Formless nectaries do not show any distinct morphological or anatomical features of the epidermis of other tissues. In some cases, nectar may be secreted through stomata (Zimmermann 1932, Galetto & Bernardello 1992) that may be abundant on the nectary (see *F. indica* below).

In SEM, crystalline structures were often seen on top of EFNs or in their immediate surrounding (Figure 3a, 4b, 4d), probably representing nectar sugar crystals. Morphology and other details of selected nectaries are described and briefly discussed for the following species (in family order):

Wrightia laevis (Asclepiadaceae)

Flattened extrafloral nectaries occur on the outer surface of sepals or on peduncles of buds and flowers. They are structurally simple, of variable shape and size (more or less circular, 30–300 µm diameter) and consist of a small number of brown coloured epidermal cells, comparable with EFNs in *Dysoxylum pettigrewianum* (see below). Nectaries of *Ichnocarpus frutescens* (Asclepiadaceae) show the same position. Non-vascularised EFNs have been described from other species of Asclepiadaceae (Satija et al. 1990).

Ipomoea indica (Convolvulaceae)

Two secretory fields occur on opposite sides of the petiole near its junction with the leaf blade, surrounded by dense indumentum on petiole and blade (Figure 2a). Each field includes ca. 100 capitate trichomes (circular, 35 µm diameter) that are singly placed in surface depressions (Figure 2b). These EFNs correspond to the simplest trichome arrangement (i.e., 'superficial nectaries' in *Ipomoea leptophylla*) in a study of 24 New

World *Ipomoea* species, contrasting with the remaining species where nectar-secreting trichomes were grouped in depressions of variable depth (Keeler & Kaul 1979). Nectar-secreting trichomes closely resemble the capitate (non-secretory) trichomes that are more sparsely scattered over the rest of the petiole and leaves. In transverse sections, trichomes consist of few-celled stalk and head tissue covered by a cuticle.

Merremia peltata (Convolvulaceae)

EFNs (Figure 2c) are similar to those of *I. indica*, but form a single continuous field around the apical part of the petiole that extends to the bases of the primary leaf veins. The surface of EFNs is glabrous, their surrounding area is glabrous to pubescent, but always more sparsely covered with hairs than *I. indica* described above. Each petiole bears several thousands of capitate trichomes (circular, 25 µm diameter), consisting of few-celled stalk tissue and few-celled globular heads.

Trichosanthes pentaphylla (Cucurbitaceae)

EFNs occur on the abaxial surface of bracts (ca. 1.5 × 1.0 mm) in leaf axils. Between three and six circular flattened nectaries (400 µm diameter) are found on each bract. Nectaries are elevated over the surrounding surface. Nectariferous tissue is composed of three layers of palisade parenchyma on top of the depressed epidermis and a second layer of subepidermal cuboidal cells (Figure 2d). The thick cuticle and has several ruptures in its central area. Nectar is probably secreted through these ruptures, as reported for other Cucurbitaceae (Muhammad 1992).

Aleurites rockinghamensis (Euphorbiaceae)

One pair of large elevated glands (≤ 5 mm) are situated on the adaxial side of the petiole at the junction with the leaf blade. These EFNs are composed of a single layer of palisade parenchyma and the epidermis. Several vessels connect the tissue below the glands with the petiolar vascular system. The same morphology was reported in earlier studies of *Aleurites* species (Groom 1894, Zimmermann 1932).

Endospermum myrmecophilum (Euphorbiaceae)

EFNs are only found on the peltate leaves of small treelets, while adult trees have very different leaves lacking EFNs (but possess hollow stems that harbour ants, Jolivet 1996). EFNs are two stalked glands with a globular head (2 mm) on opposite sides of the petiole, and 3–5 additional smaller glands in vein junctions on the abaxial leaf surface. Nectaries are vascularised and connected with the vascular system of petiole or leaf veins,

respectively. The palisade parenchyma consists of several layers (see also Zimmermann 1932).

Homalanthus novoguineensis (Euphorbiaceae)

There is one conspicuous nectary on the petiole (350 µm diameter) at the junction with the leaf (Figure 2e), and two smaller nectaries on the abaxial surface of the leaf blade adjacent to the midvein. They are typical flattened nectaries bearing a thick cuticle (15–20 µm). Ruptures may be involved in nectar secretion as in *Macaranga* (also described for *Homalanthus populifolius*; Zimmermann 1932). Several vascular strands connect the main nectary with the vascular system of the petiole.

Macaranga involucrata and *M. subdentata* (Euphorbiaceae)

In the former species (Figure 2f), EFNs occur on the adaxial leaf surface near the insertion of the petiole (two or three elliptical nectaries, 1.2 × 0.7 mm, on each side of the petiole). In the latter species (Figures 2g), one elliptical nectary, 1.0 × 1.2 mm, is found on either side. EFNs have a flat glabrous surface that is usually slightly depressed against the surrounding surface, surrounded by a distinct margin. In nearly all nectaries, one or few deep ruptures were found near the central area (Figure 2f) that extend from the cuticle well into the underlying palisade parenchyma. These ruptures are probably involved in nectar secretion; they are usually only absent on some nectaries of very young leaves that may not have commenced nectar secretion. There are two layers of palisade parenchyma above a depressed epidermis. Stomata are abundant in the area between EFNs. Flattened nectaries in *Macaranga* have been also described by Zimmermann (1932).

Rockinghamia angustifolia (Euphorbiaceae)

EFNs occur on tooth tips of serrate leaf margins. There is a distinct ‘head’ of nectariferous tissue (150 µm long) that is separated from the leaf tooth by a narrow constriction (Figure 2h). This tissue consists of one layer of very elongate palisade parenchyma around a central small-celled tissue similar to the remaining leaf tissue (Figure 3a). The small-celled tissue is vascularised.

Archidendron ramiflorum (Fabaceae: Mimosoideae)

Very large and conspicuous elevated cup-shaped nectaries (1–2 mm diameter) occur on the stem and rachis, as described by Zimmermann (1932) for *Archidendron calycinum*. EFNs are strongly vascularised, the vessels leading into a brightly coloured multilayered small-celled tissue including the epidermis (Figure 3b). This tissue is conspicuously dark brown in its central area of secretion.

Fig. 2. Scanning electron micrographs (SEM) and photographs of extrafloral nectaries from Australian rainforest plants: (a) glabrous field with nectar-secreting trichomes on leaf petiole of *Ipomoea indica*, surrounded by indumentum on petiole (top) and adaxial leaf blade (bottom) (SEM, scale bar: 1 mm); (b) close-up of trichome area of the same species (SEM, 100 µm); (c) petiolar nectary of *Merremia peltata* visited by a jumping spider (*Cytaea frotaligera*, Salticidae) foraging on the nectar; (d) transverse section through flattened nectary of *Trichosanthes pentaphylla* showing three layers of palisade parenchyma (P) on top of depressed epidermal layer (E) (SEM, 100 µm); (e) flattened nectary of *Homalanthus novoguineensis* at the junction of petiole and leaf blade, surrounded by indumentum (SEM, 200 µm); (f) flattened nectary of *Macaranga involucrata* with cuticle rupture (R) in the centre of the smooth surface (SEM, 200µm); (g) flattened nectary of *Macaranga subdentata* with crystals on top of ruptured cuticle (SEM, 200 µm); (h) elevated nectaries in *Rockinghamia angustifolia*, located on the tips of leaf marginal teeth, with distinct constriction (SEM, scale bar: 500 µm).

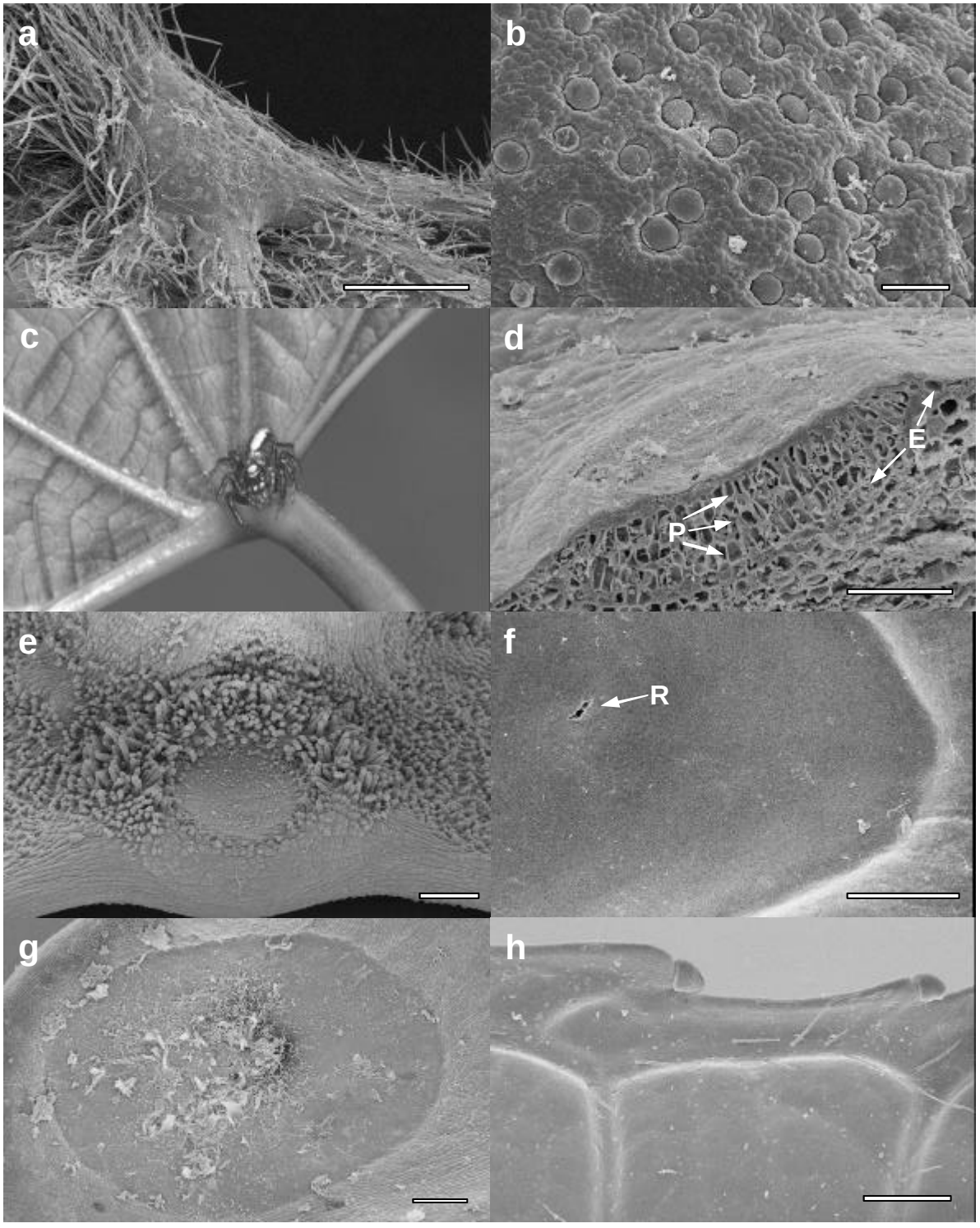


Fig. 3. Scanning electron micrographs (SEM), light microscope (LM) and photographs of extrafloral nectaries from Australian rainforest plants: (a) transverse section through nectary of *Rockinghamia angustifolia* showing palisade parenchyma (P) (LM, 100 µm); (b) transverse section through elevated nectary of *Archidendron ramiflorum* with strong vascularisation (LM, 200 µm); (c) transverse section through pit nectary on *Entada phaseoloides* stem, showing the chamber shaped by the deeply embedded epidermis (E), with a long orifice ending in a funnel-shaped opening (F) filled with crystals (LM, scale bar: 200 µm); (d) transverse section through flattened nectary on the same stem with disrupted tissue (LM, 200 µm); (e) nectaries on twig elevations of *Castanospermum australe* with a central depression (1 mm); (f) transverse section through a nectary of the same species with intact tissue on top of the elevation (LM, 200 µm); (g) leaf sheaths of *Flagellaria indica* with visiting ants (*Crematogaster* sp.); (h) nectar secreting stomata within a leaf sheath of the same species (LM, 25 µm); (i) a young compound leaf of *Dysoxylum pettigrewianum* showing the distinct bright leaf blade tip where the nectary (N_1) is situated, with a nectar foraging ant (*Anonychomyrma gilberti*), and a more mature leaflet with a dark inactive nectary (N_2).

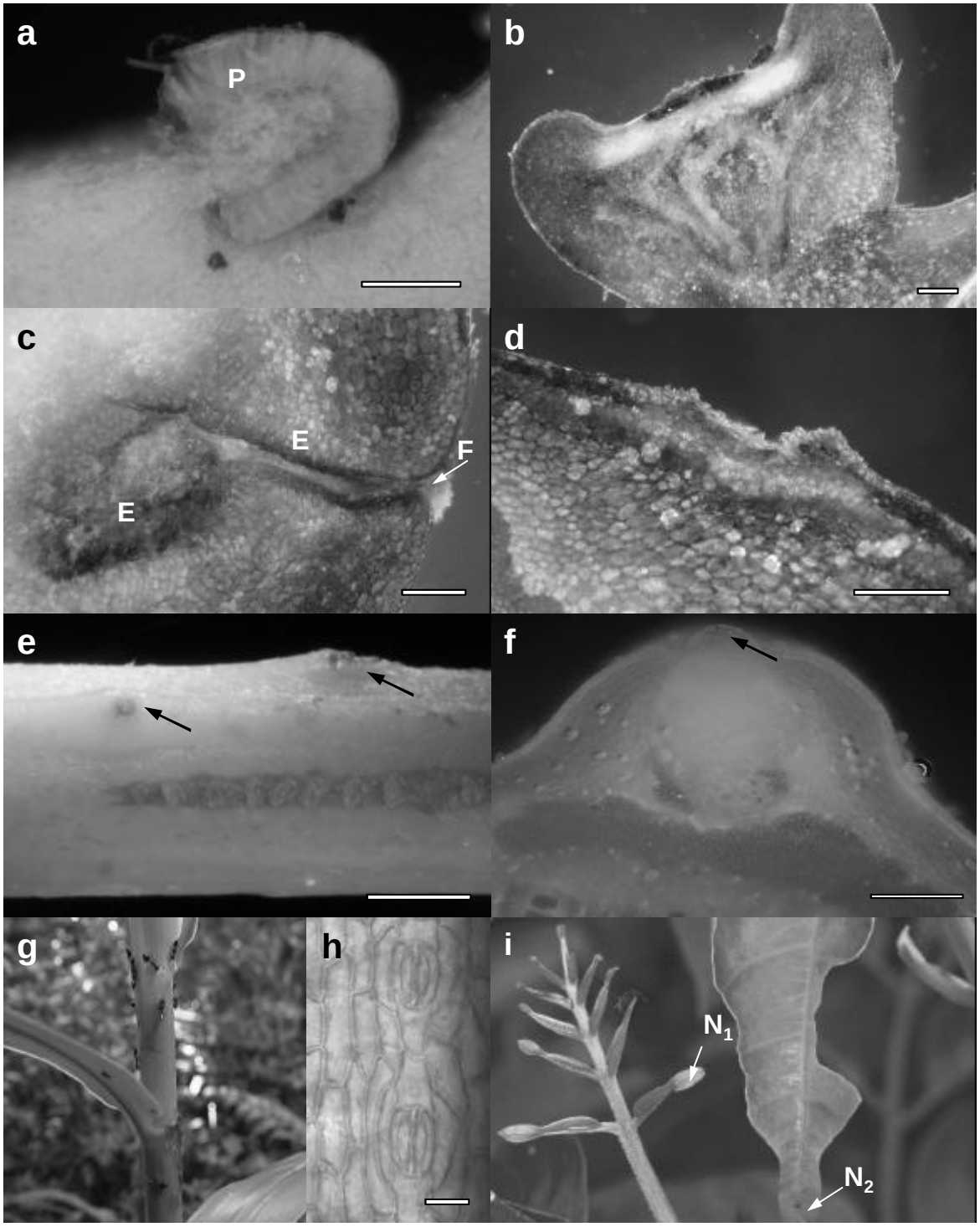
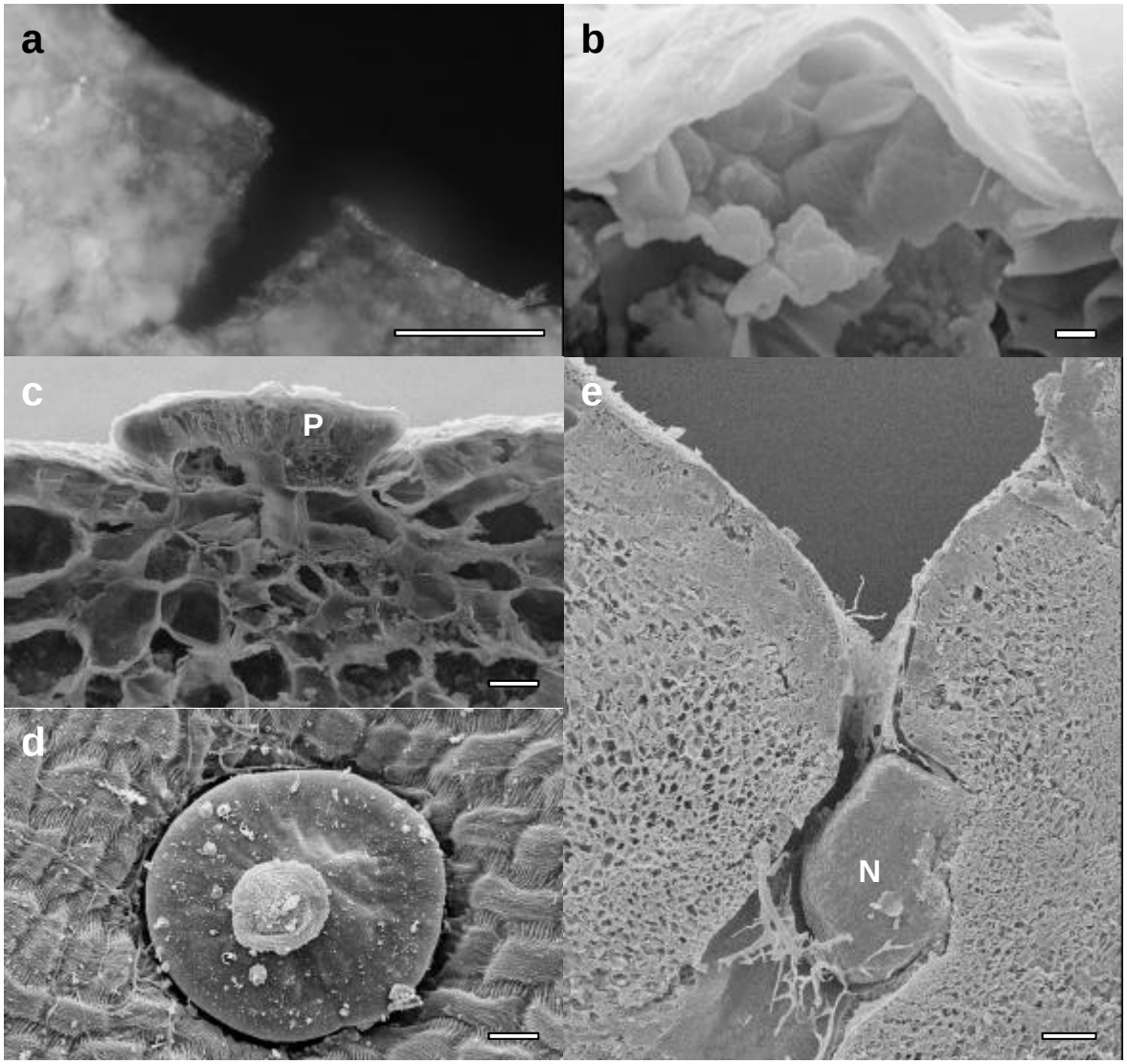


Fig. 4. Scanning electron micrographs (SEM), and light microscope photographs (LM) of extrafloral nectaries from Australian rainforest plants: (a) transverse section through a nectary of *Dysoxylum pettigrewianum* showing a deep rupture through upper tissue layers (LM, 100 µm); (b) tip of nectar-secreting capitate trichome of *Ardisia pachyrrhachis* (transverse section) with crystals accumulating under an elevated cuticle prior to disruption and nectar release (SEM, 2 µm); (c) overview of the same nectar-secreting capitate trichome showing one layer of palisade parenchyma (P) above one layer of large cells (stalk) and a depressed epidermis tissue (SEM, 20 µm); (d) trichome of the same species surrounded by abaxial leaf surface with distinctive cuticle structure (SEM, 30 µm); (e) elevated nectary (N) in a transverse cut through the leaf axil of *Syzygium* "*erythrocalyx*", with the stem on the left and leaf petiole on the right side (SEM, 100 µm).



Entada phaseoloides (Fabaceae: Mimosoideae)

EFNs occur on the stem adjacent to junctions of twigs or petioles. Nectar is secreted near the top of an elongate elevation (diameter varying from 0.2 to over 1 mm). Two different types of nectaries can co-occur on the same twig junctions: (1) Pit nectaries whose large central cavity is deeply embedded into the twig, with a long orifice (up to 300 µm long and 10 µm wide) (Figure 3c). The orifice opening is funnel-shaped (up to 50 µm wide) and depressed into the surrounding epidermis (unlike the dome-like structures in *Mimosa* and *Erythrophleum* described by Pascal et al. 2000). (2) Flattened nectaries with irregular palisade parenchyma, collapsed tissue and ruptured cuticles (Figure 3d). Additional flattened EFNs occur on a distinct bract on each inflorescence stalk basal to the flowers.

Castanospermum australe (Fabaceae: Papilionoideae)

Nectaries are scattered over the stem, rachis and leaflets, visible as elongate elevations stretching along the axis (1.5 × 0.5 mm base, 0.2 mm high) (Figure 3e). Some layers of small-celled tissue occur on top of the elevations (Figure 3f). In a later stage, this tissue is collapsed and nectar is secreted through a dark coloured depression (Figure 3e).

Flagellaria indica (Flagellariaceae)

Nectar is secreted inside the leaf sheaths that are tightly pressed against the stem (Figure 3g). No specialised tissues were found (formless nectaries). As in many formless nectaries (Zimmermann 1932), nectar is secreted through stomata that are found in relatively high density inside the leaf sheaths of this plant. The orientation of all stomata and elongate epidermal cells is parallel to the stem axis (Figure 3h). Nectaries are highly active on most plants (except saplings < 2 m) on the uppermost 2–4 leaf sheaths. EFNs in *Bambusa moreheadiana* (Poaceae) may be structurally similar. The presence of EFNs in Malaysian Bambusoideae has been recently recorded by Schellerich-Kaaden and Maschwitz (1998).

Clerodendrum tracyanum (Lamiaceae)

Nectaries are irregularly scattered over the entire abaxial leaf surface, with a higher concentration near the midvein basis. These scale-like nectaries (≤ 1 mm circular diameter) are flat-convex, the margins well elevated above the surrounding surface. EFNs are composed of 1–2 layers of irregularly shaped palisade parenchyma covered by cuticle, subtended on the inside by a single layer of cells above the epidermis. EFNs in this genus are regarded as multicellular trichomes by Zimmermann (1932), who distinguished species where ‘stalk’ tissue above the epidermis is narrower than the ‘head’ (palisade parenchyma), from species where ‘stalks’ are wider, as in the nectary described here.

Faradaya splendida (Lamiaceae)

Several flattened elongated nectaries (up to 0.8 × 1.3 mm) can be found on both sides of the leaf midvein and are restricted to the area near the midvein base. The sunken epidermis is covered by a single layer of palisade parenchyma that is more regular than in the above described *Clerodendrum*. Ruptures occur in the dark coloured central area.

Dysoxylum pettigrewianum (Meliaceae)

This species has distinctive young leaves; the incompletely opened young leaflets are often red in colour. On the tip of each leaflet, there is a flat (bright green) surface separated from the remaining basal part by a constriction of the leaflet margin (Figure 3i). One or a few EFNs occur on this adaxial surface, usually in the central area near the midvein. Most EFNs are slight depressions, others are level or slightly raised above the epidermis (± circular, irregular, ca. 70–250 µm in diameter). Some EFNs have ruptures that are several cell layers deep (Figure 4a). The irregular secretory tissue is not distinctly different in size and shape from the surrounding leaf tissue, but dark brown in colour. In other Meliaceae, described EFNs are also very simple, rather irregular and non-vascularised, but markedly elevated (*Cipadessa*: Lersten & Pohl 1985; *Guarea macrophylla*, Morellato & Oliveira 1994), and this type of nectary may be widespread in this and closely allied families (D. McKey, pers. comm.). Young leaves in the other common *Dysoxylum* species in the crane site (*D. alliaceum* Seem., *D. arborescens* Miq., *D. papuanum* Mabb., *D. parasiticum* (Osbeck) Koesterm.) lack the distinct marginal constrictions, and do not show any indication of nectar secretion.

Ardisia pachyrrhachis (Myrsinaceae)

Nectaries are mainly found on the abaxial leaf surface in an area near the base and around the midvein, and to a lesser extent on the stem. They are composed of capitate nectar-secreting trichomes (Figure 4b–d) that are inserted into depressions of the epidermis. Trichomes (diameter 130 µm, 40 µm high, distance between trichomes ca. 1–2 mm) are much larger than those of *Ipomoea* and *Merremia*. The head is composed of a single layer of multicellular palisade parenchyma (20 µm high, cuticle 0.8 µm thick), and the stalk of a layer of a few large cells (Figure 4c). Nectar is probably secreted through ruptures in the cuticle (Figure 4b). Multicellular peltate trichomes are common in the genus (Metcalfe & Chalk 1972), but their function as nectaries has not been mentioned so far.

Syzygium 'erythrocalyx' (Myrtaceae)

These trees are presently included under *S. erythrocalyx*, but they will be described as different species after a revision of the genus (B. Hyland, pers. comm.). Nearly all trees of this species in the study area are involved in a close relationship with one ant species (*Anonychomyrma gilberti*, Dolichoderinae) that inhabits the hollow tree trunks and is the main visitor of the EFNs. EFNs are hidden in the leaf axils and are not visible without dissection, but they can accumulate a nectar droplet in the narrow slit-like angle between the petiole and the stem. The nectary is an elongate elevated structure (ca. 120 µm in cross-section) that is attached to the leaf base (Figure 4e). It is composed of multiple layers of small-celled parenchyma tissue (not elongated) above a depressed epidermal layer. EFN morphology generally resembles that of the nectaries recently described for another myrtaceous species, *Chamelaucium uncinatum* (O'Brien 1995). Only the uppermost 2–3 leaf pairs of each twig have active nectaries. EFNs in leaf axils were also found in *S. cormiflorum* and *S. pseudofastigiatum*. In *S. sayeri* (F.Muell.) B.Hyland and *S. gustavioides* (F.M.Bailey) B.Hyland, active nectar secretion remains questionable and is at least not quantitatively important.

Adenia heterophylla (Passifloraceae)

There are two EFNs between the petiole and the leaf blade (one on either side of the midvein) which are concave surfaces on the secreting abaxial side (and convex from above). They represent typical flattened nectaries with a single layer of palisade parenchyma (with cuticle) on top of the epidermis. Nectaries are vascularised. Similar nectaries were described for various species of this genus, including the same species, by Zimmermann (1932).

Passiflora sp. (Passifloraceae)

This species is endemic to Queensland and briefly described by Jones and Gray (1988: 304), but has not been assigned a name so far. Two elevated EFNs are found on the petiole (usually at or below the middle of the petiole, a character of this species), and one pair of flattened EFNs on the abaxial side of the leaf blade on both sides of the midvein, slightly depressed between midvein and secondary vein. Both types of nectaries are composed of palisade parenchyma on top of the epidermis and are vascularised. Zimmermann (1932) also described both types in various species of this genus, and mentioned that at least some species accumulate nectar below the cuticle, before it breaks and releases nectar through its ruptures. This mechanism was also proposed by Durkee (1982), who studied the sugar

transport and secretion in both types of EFNs for several *Passiflora* species in greater detail.

Melicope elleryana (Rutaceae)
Several elongate EFNs (ca. 0.5 × 0.25 mm) occur on the stem of non-woody twig apices near leaf bases. They are slightly elevated above the surrounding surface that is densely coated by indumentum, with a central glabrous depression.

Discussion

The abundance of EFNs found in this study site can be considered intermediate in comparison to other tropical and subtropical countries (Table 2). Our figure of 17% of rainforest tree species bearing EFNs is comparable to results from the Amazonian forest (Morellato & Oliveira 1991), but higher than reported from Malaysia (Fiala & Linsenmair 1995) and much lower than in Panama (Schupp & Feener 1991) and Cameroon (Dejean et al. 2000). The proportion of climbing plant species with EFNs, although higher than for trees, is also considerably lower than reported from Panama and Cameroon (but note that root climbers are not included in those studies). However, biogeographical generalisations should be avoided at this stage, since these studies represent only locally restricted surveys, and different methods were applied.
The abundance of EFN-plants seems to be generally higher in disturbed forests, margins and gaps than in closed, mature rainforests (Bentley 1976, Schupp & Feener 1991, Fiala & Linsenmair 1995). Coastal rainforests in Australia such as the study site are characterised by high disturbance rates through cyclones (Adams 1994b), which may promote higher abundance of EFN-bearing pioneer shrubs, prominent examples are *Homalanthus novoguineensis* and *Macaranga involucrata.* However, vigorous climbers such as *Merremia peltata,* highly common in gaps, persisted in relatively mature stages of the forest with the same proportion of stems compared to other species. Large multibranched individuals of *M. peltata, Entada phaseoloides*, and *Ichnocarpus frutescens* were highly dominant throughout the forest and individual lianas covered several tree crowns under their dense foliage. The disturbance regime may thus contribute to the overall high abundance of climbing plants with EFNs in the entire area, but this effect was not detectable in liana stem counts between open and closed forest patches, in contrast to short-lived pioneer shrubs, where differences in stem numbers between open and closed forest were pronounced.

Table 2 Abundance of extrafloral nectaries (EFNs) in plant surveys from different tropical and subtropical habitats. Frequency of plants bearing EFNs is given as per cent species and/or individuals (cover) of vascular plants of the respective life-form.

Country	Vegetation	Life-form	Species	Cover	Reference
Australia	rainforest	trees (dbh > 10 cm)	16.9%	14.4%	(this study)
Australia	rainforest	climbing plants	21.3%	19.2%	(this study)
Brazil	cerrado	woody plants	18.8%	15.8%	Oliveira & Leitão-Filho 1987
Brazil	cerrado	woody plants	23.0%	27.6%	Oliveira & Oliveira-Filho 1991
Brazil	rainforest	trees	17.6%	19.1%	Morellato & Oliveira 1991
Brazil	forest & savanna	trees & shrubs	18.5-53.3%	29.7-50.0%	Morellato & Oliveira 1991
Costa Rica	rainforest	all plants	-	1-8%	Koptur 1992
Cameroon	rainforest	canopy trees	41.8%	55.7%	Dejean et al. 2000
Cameroon	rainforest	climbing plants (canopy)	44.4%	70%	Dejean et al. 2000
East Asia (var. countries)	transsect: tundra – subtropical forests	all plants	0.3-7.5%	10.3-40.2%	Pemberton 1998
Jamaica	second growth	(unclear)	-	28%	Keeler 1979
Korea	deciduous forest	all plants	4%	28.3%	Pemberton 1990
Malaysia	rainforest	trees & shrubs	12.3%	19.3%	Fiala & Linsenmair 1995
Panama	rainforest	woody plants	37%	16%	Schupp & Feener, cit. in Coley & Aide 1991
Panama	rainforest	small trees & shrubs	14%	-	Schupp & Feener 1991
Panama	rainforest	trees (> 10 m high)	34%	-	Schupp & Feener 1991
Panama	rainforest	climbing plants	44%	-	Schupp & Feener 1991
USA (Florida)	pine forest, hammock & savanna	all plants	8.8%	19.7%	Koptur 1992
Venezuela	rainforest	epiphytes	19%	28%	Blüthgen et al. 2000b

None of the epiphytes and root-climbers in the crane site was found to bear EFNs. True epiphytes were exclusively ferns, while root-climbers included several Araceae, *Piper* species (Piperaceae), and *Ficus pantoniana* King (Moraceae), among others. This situation is very different from that in the diverse epiphyte communities in the neotropics, where a high figure of 19% of the species of epiphytes (including climbing Araceae) were found to bear EFNs in Venezuela (Blüthgen et al. 2000b). Promising candidates for EFN-bearing epiphytes may be orchids, such as Australian *Dendrobium* species (active EFNs occur in *Dendrobium* hybrids, pers. obs.), or *Platycerium* ferns (Polypodiaceae) (Lüttge 1961), which merit closer examination.

The presence of EFNs in taxa endemic to Australia may be noteworthy in terms of the evolutionary history of the Australian rainforest. One-third of the EFN-bearing species found in this study (Table 1) are endemic to tropical Queensland, a few more species are confined to Australasia, but the majority of species are also Indo-Malayan elements. However, only two of the 29 EFN-bearing plant genera are endemic to Australasia: *Rockinghamia* (this genus comprises two species, both endemic to tropical Queensland) and *Castanospermum* (monotypic, also found in New Caledonia and Vanuatu). This generic endemism is lower than found for the entire rainforest flora of tropical Queensland, where 103 of 545 genera are considered endemic to Australia (Webb & Tracey 1981).

With the exception of these two endemic genera, all other EFN-bearing plants found at the Australian study site (including the endemic species) are from genera that display their highest diversity in South-East Asia and from which relatively few species penetrate into northern Australia. These include large genera where EFNs have not been recorded outside Australia yet (e.g. *Ardisia, Bambusa, Dysoxylum, Glochidion, Syzygium, Merremia*, each with well over 50 species worldwide). It is very likely, however, that EFNs have just been overlooked in these taxa so far, since their nectary structures are relatively inconspicuous. We are thus tempted to believe that most, if not all, EFN-bearing plants in the Australian rainforest have originated in South-east Asia. This may be associated with the colonisation capabilities of pioneer plants in general, involving many of the EFN-bearing species that typically have a much wider distribution and are rarely endemic. Evolution of EFNs may have been generally very poor in Australia compared to the pronounced radiation of myrmecochory (ant-dispersal of seeds) in arid Australian vegetation (Berg 1975). The species-rich genus *Acacia* and a few other plant species from arid habitats are notable exceptions (Lamont 1979), while EFNs are absent (or have not yet been detected) in most other primarily Australian elements, including early angiosperm families and Gondwanan relics (*Eucalyptus*, Proteaceae, Casuarinaceae, Nothofagaceae, Idiospermaceae, etc.) (pers. obs.). General conclusions about distribution and evolution of EFNs await more studies in many poorly studied floras, in Australia and elsewhere. Field surveys will be essential, since only few EFNs are obvious in herbarium specimen, while they can be more easily noted in the field by their activity in attracting ants.

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Chapter 2 – Ant community structure on nectar and honeydew sources

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Abstract

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, a concept originally derived from studies of ant communities in tropical plantations but previously not demonstrated in natural forest ecosystems. 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. Ant foraging on extrafloral and floral nectaries (involving 43 ant species on 48 plant species) was largely opportunistic, although partitioning of ant species among plant species and between canopy and understorey was significant. 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 in the dominant ants and high in many subordinate species. Both dominant ant species differed significantly in their associated species pools. 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.

Introduction

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 & Price 1992), or stochastic recruitment following disturbance regimes versus competition and niche differentiation (Tilman 1982, Hubbell et al. 1999). Among the most prominent examples of multitrophic interactions are studies about communities of herbivores (e.g. Novotny et al. 2002), pollinators (Waser et al. 1996), or frugivores (Fuentes 1995). Studies of species-rich tropical ecosystems are particularly interesting in this context (Reagan & Waide 1996). In these highly complex communities, 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 the numerical abundance and primary ecological function (Hölldobler & Wilson 1990) and economic importance (Way & Khoo 1992) of ants. Both exploitation and interference competition can be pronounced and strongly asymmetric between ant species (Fellers 1987, Savolainen & Vepsäläinen 1988, Andersen 1992, Andersen & 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) and which has since then been reported from all tropical continents (Jackson 1984a, Majer 1993). Besides the mutually exclusive distribution of dominant ants, an important second component of ant mosaics is the prediction that a specific set of ant species co-occurs with each of the dominant species (Room 1971, Room 1975, Majer 1976b, Taylor & 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 1976b, Hölldobler & Wilson 1990, Davidson 1998, Mercier et al. 1998). However, it is not known whether this tolerance mirrors a different degree of resource overlap and interspecific competition. The distribution of subdominant 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 'subdominant' ants share the same resource or habitat preferences. The actual degree of resource overlap has usually not been examined between elements of ant mosaics (Jackson 1984a, b). The question as to whether such ant mosaics are also an important structural component of diverse natural

tropical rainforests is unresolved (Floren & Linsenmair 2000, but see Dejean et al. 2000). When rainforest trees are sampled extensively, ants usually are the most abundant taxon, often including several dozen species (Wilson 1959, Stork 1991, Floren & Linsenmair 1997). The high abundance of ants is often due to a single ant colony on each tree with these dominant ant species rarely co-occurring (Stork 1991, Tobin 1995). Dominant canopy ant species belong to a limited number of genera in the tropics world-wide. They are also, by and large, the same ones that play the main role in ant mosaics known from orchards and secondary forests (Davidson 1997), thus providing some empirical evidence of the possible existence of ant mosaics in natural diverse forests.

Many community analyses, such as previous studies on ant mosaics, focus on spatial patterns by using invasive sampling techniques, such as canopy fogging, while information about the actual resource distribution and use is scarce, particularly from forest canopies (Lowman & Nadkarni 1995, Stork et al. 1997, but see bait experiments by Yanoviak and Kaspari (2000) and observations by Blüthgen et al. (2000b) and Dejean et al. (2000)). However, spatial or temporal patterns in insect samples may or may not reveal the presence of underlying processes and largely 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 & Graves 1996, Gotelli 2000, Manly & Sanderson 2002). Detailed quantitative observations on the actual resource use may be a more powerful tool 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 & Lumsden 1980, Hölldobler & Wilson 1990). The availability of a stable and rewarding resource supply worth defending may be the key factor (Jackson 1984b). Given their large biomass in forest canopies, it has been suggested that most arboreal ants may be more primary consumers than predators, since more basal positions in the food-web would allow these ants to outnumber their potential prey (Tobin 1995, Davidson 1997). For ants this usually means feeding on plant or herbivore exudates, since few ants (like leaf-cutters or seed-harvesters) are destructive phytophages. All dominant canopy ant species so far studied have been found to be omnivorous opportunistic feeders, collecting both honeydew and nectar as well as prey and other resources (Stradling 1978, Davidson 1997, Blüthgen et al. 2000b). Studies so far suggest a key role of nectar and honeydew sources for such canopy ant communities, but good empirical data are largely lacking.

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 relative 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.

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. The study area is situated in lowland rainforest 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 between September 1999 and June 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. For access to the upper forest canopy, we used the canopy crane (48.5 m tall with a jib length of 55 m).

Sampling methods

The survey of ant attendance of honeydew-producing insects, extrafloral and floral nectaries (EFNs and FNs hereafter) included observations of plants in the understorey (height above ground < 3 m; observed from the ground) and the canopy level (height 10–34 m; using the crane). Canopy plants were all located within the area covered by the crane (0.95 ha), while understorey plants were located within the same area or surrounding forest. Plants were labelled to allow repeated observations. For each survey, we recorded the identity of ant, plant, and honeydew producing insect species, and the number of ants attending nectaries or foraging for 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. Surveys in the understorey were performed during the day and night (07h – 01h), while canopy observations were restricted to daytime for logistical reasons (07h – 18h). Flower nectar use was not always unequivocal in some plants, but only those plant species are considered here where ants clearly and repeatedly showed nectar sampling behaviour. Nectar secretion of all EFNs and FNs was confirmed by glucose indicator paper (Glucostix®, Bayer), and for most nectaries also by hand-held refractometer and HPLC. In the context of this study, the analysis of honeydew use was restricted to direct trophobiosis, although cases of indirect use have been occasionally observed (ants licking droplets from the foliage underneath single Flatidae; NB personal observation). Each ant and homopteran species was collected from

several locations within the study site and subsequently identified at the Australian National Insect Collection and/or by taxonomic specialists (see Acknowledgements). Ant nomenclature follows recent literature (Shattuck 1999, Kohout 2000). Three nocturnal *Camponotus* species and all coccoids (genera *Coccus* and *Milviscutulus*) were pooled in the analysis, 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 (avoiding 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 ant species replacement is important).

The degree of interaction specificity between ants and nectar/honeydew sources was examined by four different 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) The degree of specialisation of ant species in regard to plants was calculated using Smith's measure of niche breadth (Krebs 1999) which takes resource availability into account:

$$FT_i = \sum_j \left(\sqrt{\frac{a_j}{P_i} \cdot \frac{b_j}{N_i}} \right)$$

where FT_i represents Smith's measure of niche breadth for ant i, a_j the number of plant individuals from species j visited by any ant, P_i the total number of plant individuals provided by those species visited by ant species i, b_j the number of plants from species j visited by ant species i, and N_i the total number of plant individuals visited by ant i. The width of the visitor spectrum of each plant species was calculated using the same indices but replacing ant by plant above.

(3) Niche overlap within the ant community was calculated and compared to a null model using EcoSim software (Gotelli & Entsminger 2001) (10,000 randomisations). Czekanowski's niche overlap index was applied to a reduced contingency table for EFNs and FNs (22 ant × 23 plant species, each with ≥ 5 observed interactions) as well as to the entire table for honeydew visitation; niche breadth was retained and zero states were reshuffled. Plant species were weighted by the number of individual plants found attended by ants (not

equal to column totals in most cases due to co-occurrences), and homopteran species by their number of aggregations (column totals) since they were always attended. Calculations based on equiprobable weights led to the same conclusions.

(4) For 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 (22 ant × 23 plant species). 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, subfamiliy, 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 & Entsminger 2001) (50,000 randomisations). We chose the C-score index (Stone & Roberts 1992) and fixed row and column totals (see also Ribas & 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:

$$R_s = \frac{e_1}{S_1} \cdot \frac{e_2}{S_2},$$

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 $R_s > 0$. Compared to the more commonly used turnover index

$$t_s = \frac{e_1 + e_2}{S_1 + S_2},$$

R_s may be better suited for situations where species are non-resident and only occur as visitors for a limited time: $R_s = 0$ in cases where only a subset of species recorded on the other survey is present (e.g. survey 1: species A + B, survey 2: species A), while $t_s > 0$ in such cases. (Nevertheless, conclusions for relative differences between resource groups were not affected when t_s was used instead of R_s; results not shown.) 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, respectively, using the program EstimateS 6.0b1 (Colwell 2001; 'Chao1' estimator was chosen, results from other estimators were similar; 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 (± SD) is 44 (± 2) on nectaries and 6 (± 0) on honeydew sources (EstimateS; Chao 1), 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 (± 5) and 46 (± 7), respectively). Species richness and composition of nectar feeding ant assemblages are comparable to ant collections from two canopy foggings each in a 10 × 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 which 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 (see *Chapter 5*). *Anonychomyrma* nests were only found in trunks of one common tree species, *Syzygium 'erythrocalyx'*; this close myrmecophytic relationship is mentioned by 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 (see 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: $T_{obs} = 148$, mean ± SD $T_{ran} = 134 \pm 3$, $p < 0.0001$). 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. (3) Two *Polyrhachis* species of the subgenus *Cyrtomyrma* were found to co-occur more frequently with *Anonychomyrma*, and (4) for some species, co-occurrences with dominant ants were rare. Note that these are not distinct groups and ants may be found on a continuum between them (for the classification shown in Table 2, ants were assigned to group (4) when less than two co-occurrences with dominants were found and to (2) when the ratio of co-occurrences with *Oecophylla* vs. *Anonychomyrma* was higher than 1:3 and lower than 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 (data not shown). Most ants from both (1) and (2) have been regularly observed to share the same trails on trunks and branches used by *Oecophylla* without any aggressive interaction (see Table 2). The C-score of ant species co-occurrence (234.6) is higher than that of randomly generated matrices (mean ± SD: 232.7 ± 0.8, $p < 0.01$), which would be expected when competition or other processes structure the ant community (Stone & Roberts 1992, Gotelli 2000, Ribas & Schoereder 2002).

Table 1. Ant species feeding on extrafloral nectaries (EFNs), floral nectaries (FNs), and honeydew, their nest sites, stratification, daytime activity and niche breadth. Typical nest sites: (a) arboreal and (g) ground nests. Numbers (except niche breadth) 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). Niche breadth: number of plant species visited for nectar and Smith's measure (*FT*) (95% confidence intervals in brackets).

Ant species	Nest	Stratum [1]		Activity [2]		Resource			Niche breadth [1]	
		Understorey	Canopy	Day	Night	EFNs	FNs	Honeydew	Plant spp.	*FT* [3]
DOLICHODERINAE										
Anonychomyrma gilberti (Forel)	a	25	40*	38*	1	59	6	9	20	0.95 (0.91-0.98)
Leptomyrmex unicolor Emery	g	5	11*	5	-	8	8	-	9	0.83 (0.67-0.94)
Tapinoma melanocephalum (Fabricius)	g	10*	-	10	3	10	-	-	8	0.90 (0.73-0.99)
Tapinoma minutum Mayr	-	3	-	3	-	3	-	-	3	-
Technomyrmex albipes (Smith)	a	31*	6	31	5	35	2	9	14	0.96 (0.90-0.99)
Turneria bidentata Forel	a	1	11*	1	-	9	3	-	6	0.86 (0.68-0.97)
FORMICINAE										
Camponotus "nocturnal" (3 spp.) [4]	ag	8*	-	-	9*	8	-	-	6	0.92 (0.73-1.00)
Camponotus sp1 (*macrocephalus* gp.)	a	5	-	5	-	5	-	-	3	0.95 (0.89-0.98)
Camponotus sp6 (*gasseri* gp.)		-	1	-	-	1	-	-	1	-
Camponotus vitreus (Smith)	a	14	9	13	1	22	1	-	13	0.86 (0.74-0.94)
Echinopla australis Forel	a	1	1	1	-	2	-	-	2	-
Oecophylla smaragdina (Fabricius)	a	32	65*	29	4	71	26	44	26	0.94 (0.90-0.97)
Paratrechina minutula (Forel)	ag	4	1	5	-	5	-	-	5	0.93 (0.68-1.00)
Paratrechina vaga (Forel)	ag	34*	-	29	12*	34	-	5	12	0.90 (0.81-0.96)
Polyrhachis (Cyrtomyrma) 'Cyrto 03' Kohout	a	5	5	5	-	7	3	-	7	0.95 (0.80-1.00)
Polyrhachis (Cyrtomyrma) 'Cyrto 06' Kohout	a	1	3	1	-	3	1	-	4	-
Polyrhachis (Cyrtomyrma) 'Cyrto 08' Kohout	a	2	1	2	-	2	1	-	3	-
Polyrhachis (Cyrtomyrma) 'NB5041' Kohout	a	7	8	9	-	15	-	-	8	0.92 (0.80-0.99)
Polyrhachis (Cyrtomyrma) yorkana Forel	a	6	4	7	-	9	1	-	8	0.91 (0.75-0.99)
Polyrhachis (Hagiomyrma) thusnelda Forel	a	-	2	-	-	1	1	-	2	-
Polyrhachis (Hedomyrma) cupreata Emery	a	1	1	1	-	2	-	-	2	-
Polyrhachis (Myrma) foreli Kohout	a	3	38*	3	-	24	17	-	15	0.81 (0.71-0.89)
Polyrhachis (Myrmhopla) mucronata Smith	a	1	1	-	1	2	-	-	2	-
Polyrhachis (Myrmothrinax) delicata Crawley	a	1	-	-	1	1	-	-	1	-
MYRMICINAE										
Crematogaster cf. *fusca* Smith	a	64*	17	68*	3	77	4	3	24	0.97 (0.93-0.99)
Crematogaster cf. *pythia* Forel	a	28	14	22	8	40	2	-	16	0.95 (0.89-0.98)
Crematogaster sp3	a	6	-	7	-	6	-	-	4	0.99 (0.87-0.96)
Monomorium fieldi var. *laeve nigrius* Forel	-	2	-	3	-	2	-	-	2	-
Monomorium floricola Forel	a	21*	5	20	1	23	3	-	13	0.95 (0.88-0.99)
Pheidole cf. *athertonensis*	g	3	-	3	-	3	-	-	3	-
Pheidole impressiceps Mayr	g	4	-	4	-	4	-	-	3	-
Pheidole platypus Crawley	g	29*	2	32	5	31	-	-	10	0.94 (0.87-0.99)
Pheidole sp1	g	4	-	2	2	4	-	-	4	-
Podomyrma sp1	-	-	1	-	-	-	1	-	1	-
Rhoptromyrmex wroughtonii Forel	g	11*	-	8	6*	11	-	11	6	0.95 (0.82-1.00)
Strumigenys guttulata Forel	g	1	-	3	-	1	-	-	1	-
Tetramorium insdens F.Smith	g	3	-	-	3	3	-	-	3	-
Tetramorium validiusculum Emery	g	16*	-	8	9*	16	-	-	8	0.95 (0.85-1.00)
PONERINAE										
Odontomachus ruficeps Smith	g	2	-	1	1	2	-	-	1	-
Rhytidoponera spoliata (Emery)	g	2	-	2	-	2	-	-	2	-
PSEUDOMYRMECINAE										
Tetraponera nitida (Smith)	a	2	5	2	-	6	1	-	6	0.91 (0.70-1.00)
Total (median):		398	252	383	75	569	81	81	(5)	(0.94) [3]

[1]) Restricted to visitation of EFNs and FNs 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))

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, see text (all other species were assigned to category 4). 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. gil.*	*Pol.* CyNB	*Tur. bid.*	*Tec. alb.*	*Tet. nit.*	*Mon. flo.*	*Pol.* Cy3	*Lep. uni.*	*Par. vag.*	*Phe. pla.*
Polyrhachis foreli	2*	•														
Oecophylla smaragdina	1	**14**	•													
Crematogaster cf. *pythia*	1*	**6**	**12**	•												
Crematogaster cf. *fusca*	1*	**7**	**11**	1	•											
Camponotus vitreus	2*	**5**	**5**	**7**	**6**	•										
Anonychomyrma gilberti	3	**5**	-	-	2	2	•									
Polyrhachis Cyrto'NB5041'	3	**5**	1	1	2	3	**7**	•								
Turnera bidentata	2	**4**	3	**4**	-	2	1	2	•							
Technomyrmex albipes	4	3	1	3	1	**4**	-	1	-	•						
Tetraponera nitida	1*	**4**	**5**	3	1	2	-	1	1	-	•					
Monomorium floricola	4	1	-	1	-	1	1	-	2	1	-	•				
Polyrhachis Cyrto3	2	2	1	1	3	-	3	-	1	-	-	2	•			
Leptomyrmex unicolor	2	**4**	3	1	1	1	1	-	-	1	1	-	1	•		
Paratrechina vaga	4	-	-	3	-	-	-	-	-	1	-	1	-	-	•	
Pheidole platypus	1*	1	2	1	1	-	-	-	-	2	-	-	-	-	3	•
Paratrechina minutula	4	1	-	-	1	-	1	-	1	-	-	2	1	-	-	-
Polyrhachis yorkana	2	-	1	2	1	-	1	-	-	1	-	-	-	-	-	-
Tapinoma melanocephalum	4	-	-	1	1	-	-	-	-	-	-	1	-	-	2	-
Camponotus sp1	4	-	-	1	-	1	-	-	-	1	-	1	-	-	-	-
Polyrhachis Cyrto6	3	-	-	-	-	-	3	-	-	-	-	1	-	-	-	-
Tapinoma minutum	4	-	-	-	-	-	-	-	-	-	-	1	-	-	1	1

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 *Chapter 1* 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 tree) were observed on EFNs (Table 1). On all EFN-bearing plant species, ants were the most common nectar consumers and constitute more than 90% of the total arthropod individuals observed feeding. EFNs were located on the foliage or on inflorescences (including circumfloral nectaries), but outside the flowers.

Flower nectar use by ants was observed on 14 plant species (Table 3), 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). 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 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 secretions on palm inflorescences (from flower abscission scars on *Normanbya normanbyi* and wounds in

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. 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	Lifeform	Stratum	*N*
a) Extrafloral nectaries				
ASCLEPIADACEAE	*Wrightia laevis* subsp. *millgar* (Bailey) Ngan	tr	c	2
	Ichnocarpus frutescens R.Br.	cl	c	9
CONVOLVULACEAE	*Ipomoea indica* (Burm.) Merr.	cl	u^{+}	19
	Merremia peltata Merr.	cl	u^{+} c	67
EUPHORBIACEAE	*Endospermum myrmecophilum* L.S.Sm.	tr	u^{+}	11
	Glochidion philippicum (Cav.) C.B.Rob.	tr	c	1
	Homalanthus novoguineensis (Warb.) K.Schum.	sh	u^{+}	28
	Macaranga involucrata subsp. *mallotoides* (F.Muell.) L.M.Perry	sh	u^{+}	45
	Mallotus mollissimus (Geiseler) Airy Shaw	sh	u	4
	Rockinghamia angustifolia (Benth.) Airy Shaw	tr	u c	7
FABACEAE *s.l.*	*Castanospermum australe* A.Cunn. & Fraser ex Hook	tr	c	4
	Entada phaseoloides Merr.	cl	u^{+} c	27
FLAGELLARIACEAE	*Flagellaria indica* L.	cl	u^{+} c	79
LAMIACEAE	*Clerodendrum tracyanum* (F.Muell.) F.Muell. ex Benth.	sh	u	5
MELIACEAE	*Dysoxylum pettigrewianum* F.M.Bailey	tr	u c	9
MYRSINACEAE	*Ardisia pachyrrhachis* (F.Muell.) F.M.Bailey	sh	u^{+}	17
MYRTACEAE	*Syzygium* "*erythrocalyx*" B.Hyland	tr	u^{+} c	14
SMILACACEAE	*Smilax* cf. *australis*	cl	u^{+}	6
(b) Floral nectaries				
ARECACEAE	*Archontophoenix alexandrae* (F.Muell.) H.Wendl. & Drude [1])	pa	c	3
	Licuala ramsayi (F.Muell) Domin	pa	c	6
	Normanbya normanbyi (W.Hill) L.H.Bailey [1])	pa	c	12
BIGNONIACEAE	*Neosepicaea jucunda* (F.Muell.) Steenis	cl	c	1
ELAEOCARPACEAE	*Elaeocarpus angustifolius* Blume	tr	c	3
EUPHORBIACEAE	*Rockinghamia angustifolia* (Benth.) Airy Shaw	tr	c	1
FABACEAE *s.l.*	*Entada phaseoloides* Merrill	cl	c	6
LAURACEAE	*Cryptocarya hypospodia* F.Muell.	tr	c	1
	Cryptocarya murrayi F.Muell.	tr	c	4
MELIACEAE	*Dysoxylum mollissimum* subsp. *molle* (Miq.) D.J.Mabberley	sh	u	1
	Dysoxylum papuanum Mabb.	tr	c	2
	Toona ciliata M.Roem	tr	c	1
MENISPERMACEAE	*Pachygone longifolia* F.M.Bailey	cl	c	3
	Stephania japonica (Thumb.) Miers	cl	c	1
MYRSINACEAE	*Ardisia pachyrrhachis* (F.Muell.) F.M.Bailey	sh	u	1
	Embelia caulialata S.T.Reynolds	cl	c	1
OLEACEAE	*Jasminum didymum* G.Forst [2])	cl	c	1

[1]) including wound sap, [2]) postfloral nectar

Archontophoenix alexandrae) were pooled with true flower nectar use in these plants, and postfloral nectar of *Jasminum didymum* was available to ants after corolla abscission.

The distribution of nectar-feeding ant species on plant species was significantly different from random (T_{obs} = 807, mean ± SD T_{ran} = 703 ± 13, $p < 0.0001$). Because $T_{obs} > T_{ran}$, the ant–plant matrix can be considered compartmentalised, i.e. ant species were significantly partitioned across plant species.

A broad range of EFN- and FN-plants was usually visited by each ant species (median: 5, quartiles: 2–9) (Table 1). Niche breadth was very high in nearly all species (FT_A; median: 0.95, quartiles: 0.91–0.98) and trophobiotic ant species (the six ant species found to forage on honeydew, Table 1) did not differ significantly from the rest of the ant community (Mann-Whitney U test: $Z = 0.26$, $p = 0.80$). From the plant's viewpoint, number and niche breadth of ant visitors is similarly high (ant species: median: 3, quartiles: 1–7; FT_P: median: 0.90, quartiles: 0.85–1.00); variation between EFNs and FNs was not significant ($Z = 1.26$, $p = 0.21$). Niche overlap for the ant community (mean Czekanowski index: 0.242; 22 ant × 23 plant species) was significantly greater than for randomly organised matrices (mean ± SD: 0.204 ± 0.007, $p < 0.0001$). Overall niche partitioning would lead to lower than random overlap, so this result indicates that such processes may not extend through the entire structure of the nectar feeding ant community. However, mean variance of niche overlap (0.025) was significantly greater than expected by chance (0.016 ± 0.002, $p < 0.0001$), indicating that some 'sub-guilds' of similar preferences may be distinguished (see Albrecht & Gotelli 2001). Niche overlap between *Anonychomyrma* and *Oecophylla* (0.222; 35 plant species) was significantly smaller than expected (0.394 ± 0.057, $p < 0.001$).

Factorial effects in the ordination of ant plant associations are summarised in Table 4. No significant segregation of ant subfamilies was found and no significant separation of ant species that were involved in trophobiosis or not. Between ant mosaic compartments (common cooccurrence with either *Oecophylla* or *Anonychomyrma* or both; categories 1-3, see 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 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 × 32 plant species, ≥ 3 interactions); for a reduced table (14 × 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; $T_{obs} = 1960$, $T_{ran} = 1838 \pm 5$, $p < 0.0001$). 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).

The number of passing ant individuals attracted to EFNs and FNs per plant varied between plant species (Figure 1a) and ant species (Figure 1a), ranging between a single or very few ants (in many cases) to ca. 100 ants (rare). The two dominant ants were among the species with the highest recruitment per plant.

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 1). 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). Overall differentiation of all ant species on EFNs between day and night was significant ($T_{obs} = 1292$, $T_{ran} = 1248 \pm 4$, $p < 0.0001$). Few species deviated significantly from the total activity pattern, most notably a pooled group of nocturnal *Camponotus* species (Table 1).

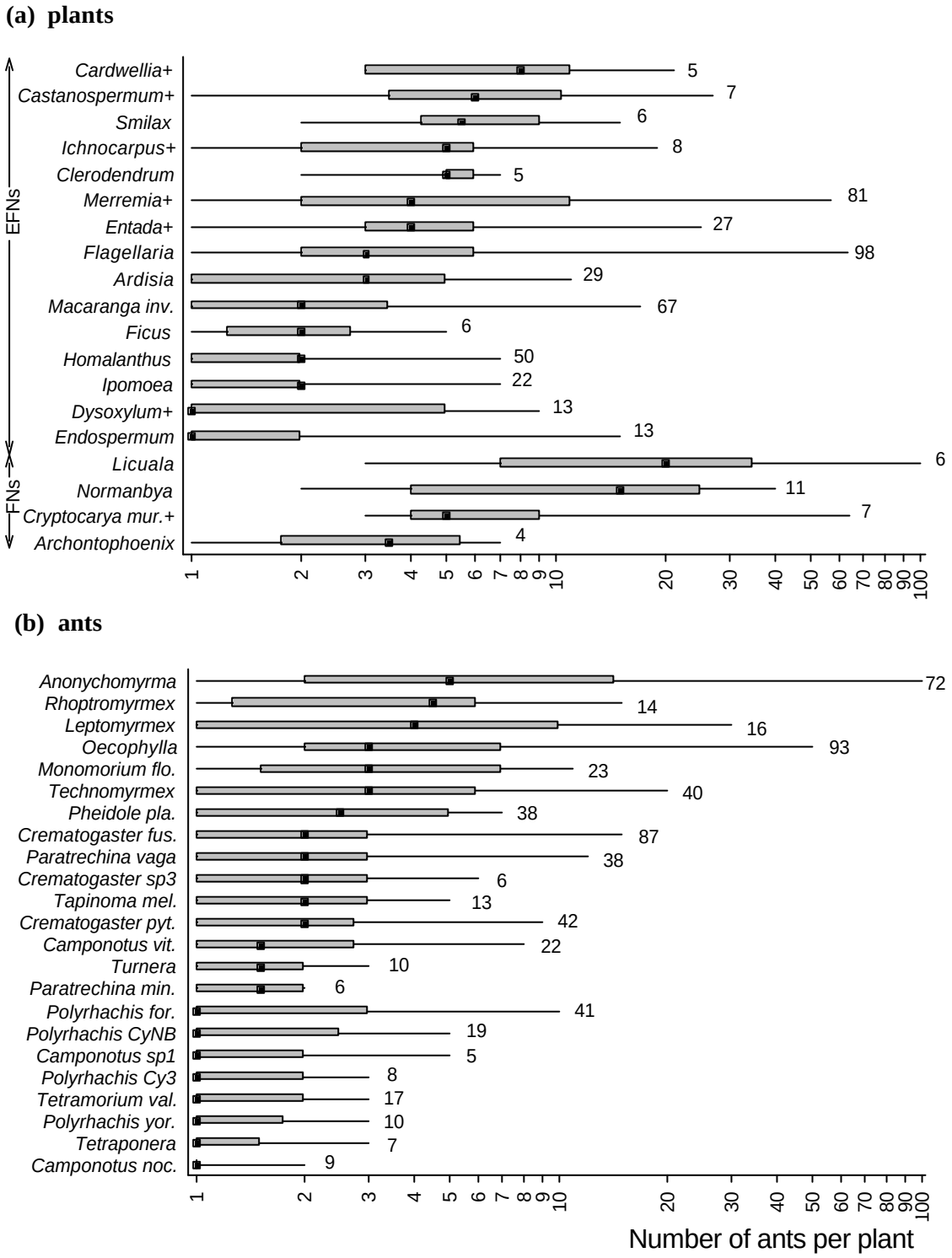


Fig. 1 Number of ant individuals per plant foraging on extrafloral and floral nectaries (EFNs and FNs), plotted on logarithmic scale, (a) by plant species (only those with a minimum of 3 vs. 5 observations of FNs vs. EFNs, respectively), (b) by ant species (minimum 5 observations). Box plots display medians (black square), quartiles (grey box), and range (whiskers). Numbers of observations shown for each species. Plant species where foliage or flowers could only be partly examined for each individual (and thus number of ants may be underestimated), are marked with '+'. Full species names are given in Table 1 and 3.

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
Subfamily [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

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 frequent (Table 1) and abundant (Figure 1) visitors of EFNs and FNs. 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, see *Chapter 5*). 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* (for details see *Chapter 4*). 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_{obs} = 262, T_{ran} = 218 ± 3, $p < 0.0001$; all coccoids pooled). Mean Czekanowski niche overlap of the community (0.204) was not significantly different from random (0.165 ± 0.055, $p = 0.20$), but mean variance (0.099) was significantly higher

(0.048 ± 0.025, $p = 0.03$). Niche overlap between *Anonychomyrma* and *Oecophylla* (0.121) was significantly smaller than expected (0.253 ± 0.071, $p = 0.03$). These niche partitioning analyses can be considered conservative due to the pooled group of coccoids. *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 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, see *Chapter 5*). 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). Thus, for any colony of *Oecophylla* and *Anonychomyrma*, the number of workers collecting honeydew may be typically 10–100 times as high as nectar collecting workers. 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).

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.

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

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

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 (Figure 2a). 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 (Figure 2a); the proportion of all surveys (including those with a single ant worker) was 23%. Variation among ant species was similar (Figure 2b), ranging from 9% to 100% (total for all ant species: 46%). The two dominant ants showed low proportions of co-occurrences. Those ants that rarely co-occurred with dominants (above category 4) were also characterised by rare co-occurrences in general. In turn, co-occurrences represent large proportions of the visits for several subordinate ant species typically found in territories of the dominants, significantly higher than expected in four species (Figure 2b). There was a 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). Furthermore, co-occurrence frequency and niche breadth of ant species were negatively correlated ($r_S = -0.48$, $p = 0.02$, $n = 22$ ant species), thus no evidence was found that increased plant specialisation could reduce co-occurrences in the nectar feeding ant community. The proportion of co-occurrence is largely interchangeable with other measures of ant species diversity: the percentage of ant species co-occurrence was linearly correlated with the mean Shannon-Weaver-index of ant diversity ($r = 0.95$, $p < 0.001$, $n = 23$ plant species) as well as with mean Evenness ($r = 0.99$, $p < 0.001$).

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 c^2 column indicate significant differences between resources in frequency of ant co-occurrence or replacement, respectively (c^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.	c^2	n_2	$R_s = 0$	$0 < R_s < 1$	$R_s = 1$	c^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**

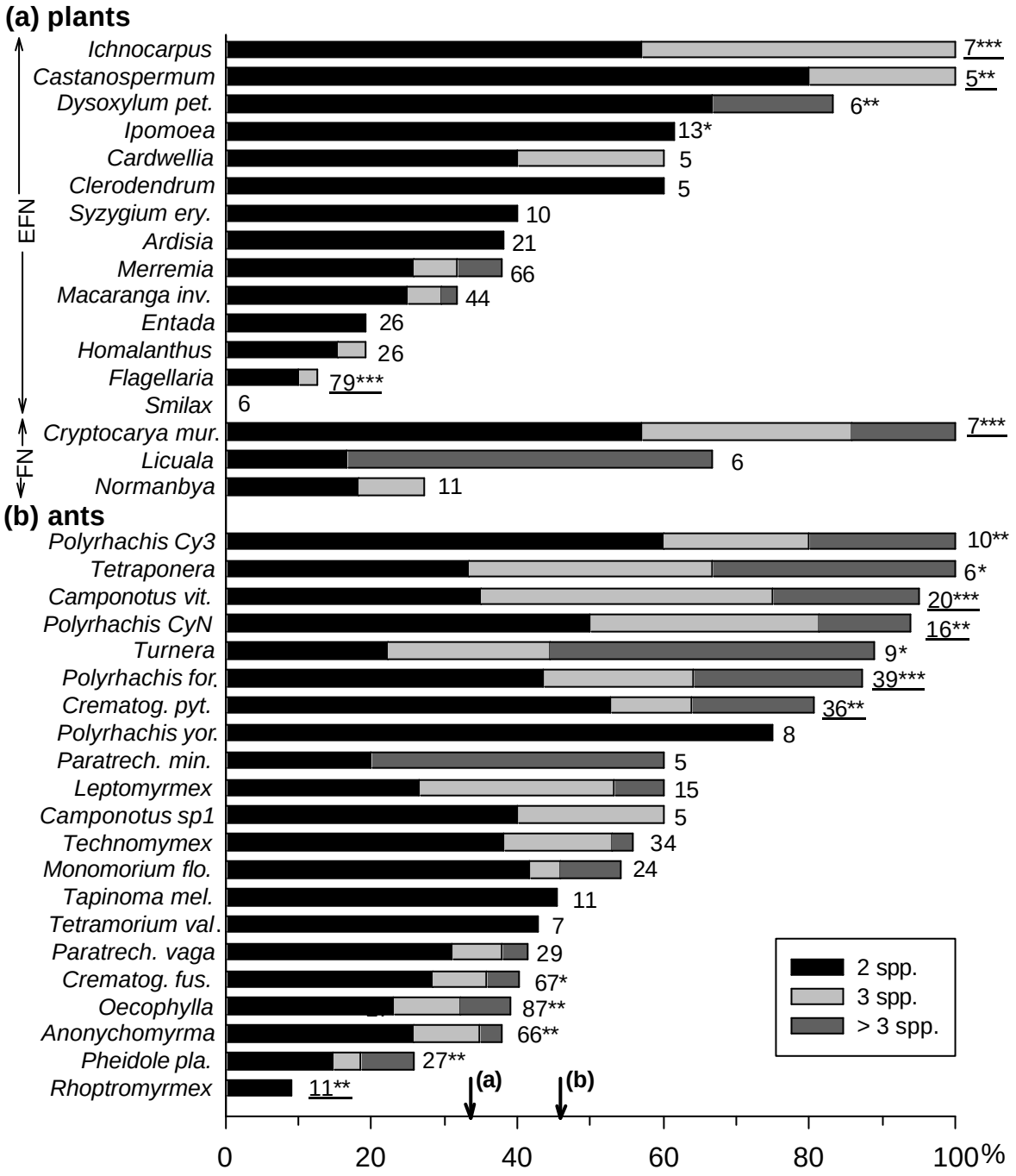


Fig. 2. Frequency of co-occurrence of two, three or more ant species on the same plant (a) by plant species with extrafloral or floral nectaries (EFNs or FNs) and (b) by ant species. Only surveys with at least two ant individuals and species with a minimum of five observations considered; number of surveys per plant species displayed after each bar. Significant deviation from the mean proportion of two or more co-occurring species (indicated by an arrow on the x-axis) is indicated by *, **, or *** ($p<0.05$, $p<0.01$, $p<0.001$; c^2-test, observed against expected frequencies), significant values after sequential Bonferroni correction underlined. Full species names are given in Table 1 and 3.

Discussion

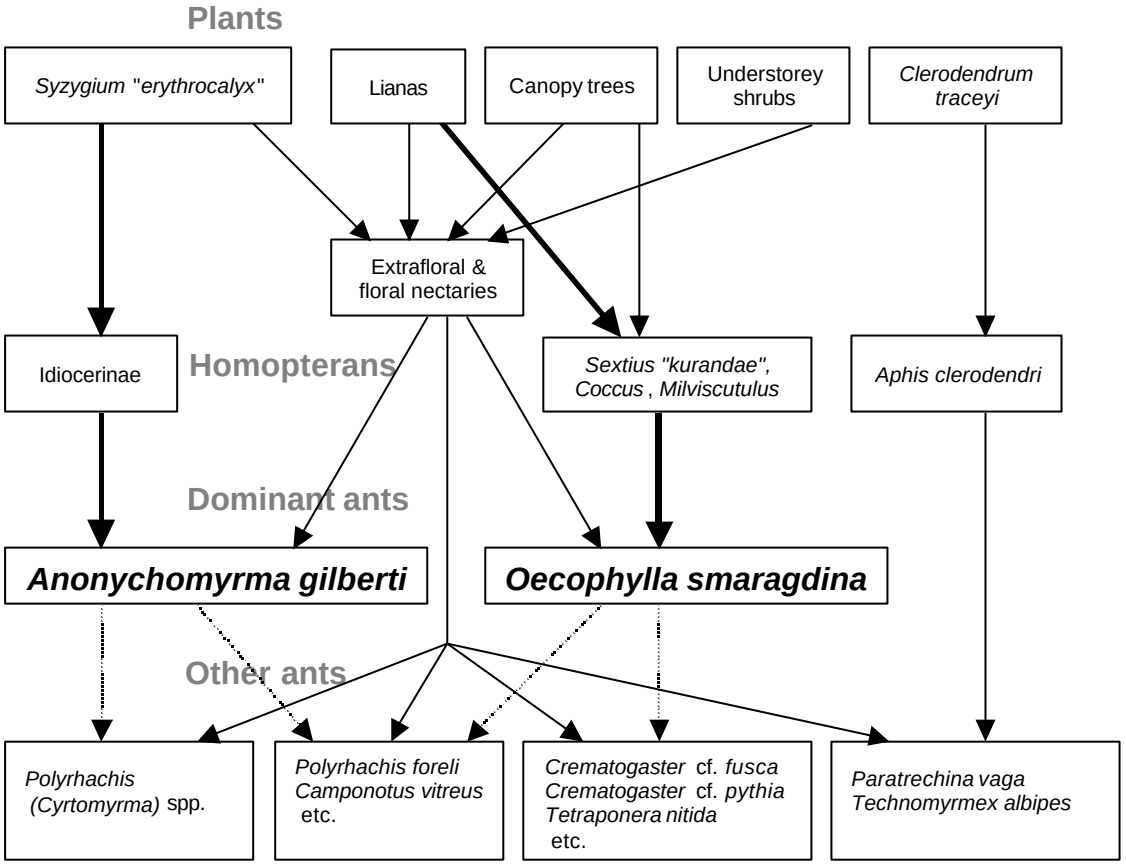
Most arboreal ants are at least partly carnivorous (Jeanne 1979, Floren et al. 2002), but honeydew and nectar represent key resources as well (Tobin 1995, Davidson 1997) and are obviously more predictable than prey (Jackson 1984b, Yanoviak & Kaspari 2000). The importance of honeydew and nectar could 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 (*Chapter 7*). Differences between honeydew and nectar utilization were pronounced at our Australian 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 & Brandão 1991, Blüthgen et al. 2000b). Non-aggressive co-occurrence of different ant species was common, and assemblages on individual plants were temporally variable. Partitioning of ant species on nectar secreting plant species was significant between 'sub-guilds', but not strong throughout the entire community.

(2) The ant community on honeydew sources was substantially different: co-occurrence was completely 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 (see also *Chapter 5*), or by a colony representing one of four ant species in the understorey. Reduced diversity and higher territoriality of honeydew-foraging ants appear to be more or less ubiquitous as previously found in other ecosystems (e.g. Brian 1955, Dejean et al. 1997, Blüthgen et al. 2000b).

Between the two dominant ants, niche overlap between nectar sources and between honeydew sources was significantly lower than expected by chance. The distinct compartmentalisation of honeydew and nectar sources may result in a cascade of effects, visualised in Figure 3. 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 (*Chapter 5*) 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 (see also Monteith 1986) (some

Fig. 3. Model visualising the main elements of the investigated multitrophic food web and proposed 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.



were inhabited by *Crematogaster* cf. *fusca*, NB unpublished observations). The assemblage of hierarchically inferior ant species may then be affected 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 subdominant 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 & Vepsäläinen 1988, Andersen 1992, Perfecto 1994) and ant mosaic studies (Room 1971, Room 1975, Taylor & Adedoyin 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 & Lumsden 1980, Jackson 1984b; see also myrmecophytes: Davidson & McKey 1993). Spatial structure may be important here, since typical honeydew sources may be 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 & Gotelli 2001, Hossaert-McKey et al. 2001), although such mechanisms were certainly not important in the system studied here where most ants were more or less continuously active (except for a group of nocturnal *Camponotus* species).

(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) and may be important for other ephemeral resources. 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 are monopolised by dominant ants in the long run.

(4) The more predictable a resource, the more beneficial it should be to monopolise it. Tropical litter ant communities may be very unstable and there is little evidence of

interspecific competition for food (mostly prey) (Kaspari 1996b, Yanoviak & 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 could be 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 (see Percival 1961, Baker et al. 1978).

If nectar indeed represents a poorer resource than honeydew, monopolisation should be less economical. However, while trophobiosis may represent a distinct type of resource use where specialisation affects co-occurrence patterns (for lycaenids with specific ant associations, see Seufert & Fiedler 1996), more gradual but non-negligible variability between nectar sources may reveal independent information about a direct correlation between resource quality and visitation. Some plants, such as *Flagellaria* and *Smilax*, continuously offer large amounts of nectar and attracted many ants that were often from one of the two dominant ants which then defended the plant against competitors (Figures 1, 2). Nectar from these two species is characterised by a high concentration and a broad spectrum of amino acids, similar to honeydew (*Chapter 3*). In contrast, typical nectar plants were not monopolised, even where high numbers of ants have been attracted (there was a positive relationship between number of ant individuals and species). Moreover, co-occurrence was more common on flowers than on extrafloral nectaries. Flower nectar was much more restricted in time and space than extrafloral nectar and may be generally less important for ant nourishment (documented by a lower abundance of ant-visited plants and lower proportion of ants compared to all nectar-foraging arthropods). However, visitation to relatively short-lived flowers was unlikely limited by recruitment capacity or competitive ability of ants, since ants are generally very rapid and dominant in response to baits or other resources. The hypothesis initiated by Janzen (1977) and put forward or controversely discussed by others (e.g. Haber et al. 1981, Ghazoul 2001) that ants may be largely discouraged from tropical flowers by chemical or mechanical repellents, was not supported by our observations: cases where ants did use flower nectar were more common here than cases where ants did not. Examples of the latter group included flowers with long

and narrow tubes that obviously prevented most ants from nectar access, and *Syzygium gustavioides* and *Acmena graveolens* (both Myrtaceae), where nectar was not observed to be consumed from relatively accessible flowers, but was accepted (albeit not eagerly) when offered outside the flowers (NB unpublished observations). Thus, floral ant repellents other than narrow tubes may be either rare at the study site, or they may be more gradual in that they did not completely hinder ants from using nectar but only prevented massive ant recruitment. In general, the observed under-representation of ants on nectar producing flowers (although often supplied in large amounts) in comparison to EFNs or honeydew sources, may reflect a poorer nectar quality.

Specialisation

Trophobiotic interactions in our study 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, and homopterans in particular may often depend on this mutualism, which may drive specialisation processes. Other trophobiotic systems may be less specific and more opportunistic (e.g. Stadler & Dixon 1998), as is the rule for temperate zone systems where seasonality prevents stable long term associations. 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. 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 (NB unpublished observations), although other more obligate trophobioses may not allow for ant interchange (lycaenids: Fiedler et al. 1996, Seufert & 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 & 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 & 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.

In summary, our study demonstrated a distinct ant mosaic in the tropical Australian forest consisting of two mutually exclusive dominant ant species and an assemblage of co-occurring subordinate species, with some of these subordinate species occurring exclusively with only one of the two dominant ant species, while others overlap. In order to understand the processes causing this pattern, it is important to integrate ant behaviour (communication specificity, aggressiveness, recruitment), ant nutritious requirements and resource availability (quality, preferences, temporal and spatial dynamics). The high plasticity of resource use in ants, in particular the differential visitation of honeydew and nectar sources, may be a key driver of this community.

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Chapter 3 – Sugar and amino acid composition of nectar and honeydew

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Abstract

Ants (Hymenoptera: Formicidae) consume a broad spectrum of liquid food sources including nectar and honeydew, which play a key role in their diet especially in tropical forests. This study compares carbohydrates and amino acids from a representative spectrum of liquid sources used by ants in the canopy and understorey of a tropical rainforest in northern Queensland, Australia. 18 floral nectars, 16 extrafloral nectars, two wound sap and four homopteran honeydew sources were analysed using high performance liquid chromatography (HPLC). Wounds comprised flower abscission scars on *Normanbya normanbyi* L.H.Bailey and bitemarks on *Cardwellia sublimis* F.Muell where ants were actively involved in wounding. Discriminant analysis was performed to model differences between food sources in sugar and amino acid concentration and composition. All characteristics varied significantly between plant species. Honeydew contained a broader spectrum of sugars (melezitose, raffinose, melibiose, lactose and maltose) than nectar (sucrose, glucose, fructose), but certain extrafloral nectars had similar amino acid profiles and were often monopolised by ants like honeydew sources. Most common amino acids across the sources were proline, alanine and threonine among 17 a-amino acids identified. Interspecific variability concealed characteristic differences in sugar and amino acid parameters between nectar, honeydew and wound sap across all plants, but these types differed significantly when found on the same plant. Among all sources studied, only few flower nectars were naturally not consumed by ants and significantly less attended than sugar controls in feeding trials. These nectars did not differ in sugars and amino acids from ant-attended flower nectars, suggesting the activity of repellents. Apart from these exceptions, variability in amino acids rather than carbohydrates is proposed to play a key role in ant preferences and nutrition.

Introduction

Nectar (sugary plant secretions) and honeydew (excretions from herbivorous insects) are two important liquid food sources utilized by a broad spectrum of animals (Zoebelein 1956, Faegri & van der Pijl 1979, Koptur 1992). In turn, animal attraction often results in a reward to the producer. Common benefits for the plant include pollination (flower nectar) or protection against herbivores through attraction of their predators or parasitoids (extrafloral nectar) (Schemske 1980, Pleasants & Chaplin 1983, Beattie 1985, Hespenheide 1985, Koptur 1992), while services for the honeydew-producer include protection against parasitoids or predators (Buckley 1987, Del-Claro & Oliveira 2000). Besides such clearly mutualistic interactions, benefits are not ubiquitous (Whalen & Mackay 1988, Bach 1991) and even cases of parasitism are known where nectar or honeydew are consumed without any reward, such as nectar-robbing by non-mutualistic animals from floral (Herrera et al. 1984) or extrafloral nectaries (Horvitz & Schemske 1984, DeVries & Baker 1989).

From the consumer's perspective, both the quantity and quality of resources may be crucial for foraging decisions. Nectar and honeydew are per definition composed of sugars, but nearly all of these sources also contain various amino acids (Baker et al. 1978). These are the main nutritious substance classes, while other compounds (lipids, proteins, fatty acids etc.) are usually much less common (Baker & Baker 1983). For foraging preferences of animals, total sugar concentration (Adler 1989, Blem et al. 2000) and sugar identities (Koptur & Truong 1998, Romeis & Wäckers 2000) are important, but amino acids play a key role as well for some consumers (Inouye & Waller 1984, Erhardt 1991, Lanza et al. 1993, Gardener & Gillman 2002) albeit not for all (Romeis & Wäckers 2000). Most of these preferences have been found under experimentally controlled conditions, while natural environments can be much more complex and preferences observed in the laboratory may not translate into actual resource visitation preferences in the field (see Gottsberger et al. 1984). Nectar and honeydew usually function as fuel for adult metabolism or as complementary food rather than as complete diets, but nevertheless fitness benefits from feeding on nectar or honeydew can be pronounced (Adler 1989, Hainsworth et al. 1991, Fiedler & Saam 1995, Fischer & Fiedler 2001). It is unclear to what extent the sources fully satisfy the animal's requirement of essential amino acids (see Beattie 1985, Fischer & Fiedler 2001).

In order to link the supply by producers and the demand by consumers, an important baseline is to analyse the composition of a full spectrum of available resources. Such attempts on the community level are scant, since nectar analyses are often motivated by

evolutionary or taxonomical hypotheses rather than from an ecosystem perspective (Baker & Baker 1973, Gottsberger et al. 1984, Nicholson & Van Wyk 1998), and honeydew analyses are usually focused on a small set of plant or homopteran species (Douglas 1993, Völkl et al. 1999).

In this study we present an analysis of a representative selection of plant-derived liquid food sources consumed by the ant community of a tropical Australian rainforest. These sources include honeydew, extrafloral nectar, floral nectar and wound sap. Ants are by far the dominant consumers of the first two sources in many ecosystems (Beattie 1985, Buckley 1987, Blüthgen et al. 2000b), while flower visits by ants may be less common (Janzen 1977, but see Rico-Gray 1993) and wound sap use has been poorly documented thus far (Tobin 1994). The objective of our study was (1) to compare the concentration and composition of sugars and amino acids from food sources consumed by ants, (2) to test whether unvisited sources differ in these parameters and whether they are unpalatable or otherwise protected against ants, and (3) to examine whether ant crop contents match the composition of the sources on which ants are observed to feed.

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. The study area is situated in lowland rainforest 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). Nectar and honeydew samples were collected between September 1999 and June 2002. During this time, most parts of the forest were in an early stage of recovery from category 3 cyclone 'Rona' in February 1999 when large parts of the canopy had been severely damaged. For access to the upper forest canopy, we used the canopy crane (48.5 m tall with a jib length of 55 m).

Sampling methods

Nectar was sampled directly from nectaries using 1 µl and 10 µl microcapillary tubes, usually after ant exclusion over night using sticky resin (Tanglefoot) on branches or by plastic bags where amounts were insufficient to allow direct sampling. No attempt was made to emasculate flowers prior to sampling, so that samples represent (older) nectar as encountered by visitors (potentially including diluted substances from pollen or flower tissue) rather than pure glandular secretions by the plant (see Gottsberger et al. 1990). Honeydew samples were collected from homopteran aggregations that were either isolated by plastic bags

over night on the intact twig, or carried into the lab on twig cuts in a vase, from which honeydew dropped onto a plastic plate underneath the homopterans. Samples collected in 2001 were stored frozen in the microcapillaries until dilution in 70% ethanol and subsequent analysis, those collected in 2002 were immediately transferred into tubes with 70% ethanol solution with sterilised water after collection. The two sampling methods did not significantly affect the qualitative and quantitative results (pairwise t-tests on mean number and concentration of sugars and amino acids for 12 species: all $t < 0.6$, $p > 0.5$; concentration of single sugars and single amino acids except alanine: all $t < 2.1$, $p > 0.06$; samples from 2001 had slightly higher alanine content: $t = 2.3$, $p = 0.04$). Therefore, analyses from both years were pooled.

Analyses of ant crop content included pooled samples from 5–15 workers observed directly at or close to a specified food source. By gently squeezing their body, ants with filled crops (expanded gasters) regurgitated a clear fluid that was directly sampled with microcapillary tubes. Cloudy regurgitates indicating pollution by hemolymph were discarded.

Analysis of sugars and amino acids

Total sugar concentration of some samples was measured directly on site to the nearest 0.5% sucrose concentration equivalent (°Brix) using a handheld refractometer (Eclipse, Bellingham & Stanley). Ethanolic samples were vacuum centrifuged, diluted in pure ion-free water, filtered (Spartan 3/20, 0.45 µm pores, Schleicher & Schuell) and divided for separate sugar and amino acid analysis by high performance liquid chromatography (HPLC) (Waters autosampler 717+, CHM column heater module). Sugar analysis was performed with an isocratic pump (Waters 510), Sentry Guard column (high performance carbohydrate, 3.9 × 20mm), Waters high performance carbohydrate column (4.6 × 250 mm), solvent (72:28 acetonitrile:water mix) and refractive index detector (Waters 410; flow rate 1.4 ml min^{-1}). Amino acid samples were derivatised (6-aminoquinolyle-N-hydroxysuccinimidyle-carbamate in borate buffer) and analysed using Waters 600E pump, Sentry Guard column (NovaPak C_{18}, 3.9 × 20 mm), Waters AccQtag column (3.9 × 150 mm), trinary solvent system (TEA/phosphate buffer with pH 5.5, acetonitrile and water) and fluorescent detector (Waters 470; flow rate 1 ml min^{-1}). HPLC was controlled and data obtained using Waters Millenium 3.0 software. Ten carbohydrates and 17 α-amino acids were used as standards every 10 samples. Total sugar and total amino acid concentrations and relative proportions of single compounds were calculated only from those substances that were identified.

Feeding trials

In order to test palatability of nectar from unvisited flowers, we extracted nectar from flowers, and offered 10 µl nectar drops in plastic tubes (lids of standard microcaps; nectar was kept frozen until the experiment). A 10 µl control solution contained a 1:1 mixture of glucose and fructose in the same concentration as the nectar (confirmed with refractometer). Five pairs of nectar and control tubes were tied to tree trunks with regular traffic of *Anonychomyrma gilberti* ants, and this experiment was repeated on a different trunk on the following day (total $n = 10$ for each test). The number of ants were counted at each treatment every 5 min for at least 1h or until one of the treatments was empty (time intervals between surveys exceeded the typical duration of individual ant visits). Only those ants were counted that unambiguously consumed the test nectar or control solution (mouthparts stayed > 2 sec in liquid). The mean number of ants for all surveys with at

least one ant present was taken as measure of palatability and compared between treatment and control in a pairwise test (Wilcoxon matched pairs).

Data analysis

Four different kinds of secretions were distinguished and henceforth denoted as 'food types': extrafloral nectar (including circumfloral nectaries), flower nectar, wounds, and honeydew (excretions from ant-tended homopterans). For some plant species, different food types occurred on the same plant. Different plant species plus different secretion types were thus treated as 39 distinct units as listed in Table 1 and defined as 'food sources'. For each food source, mean values were calculated from different plant individuals (which were each represented by their mean if replicates were taken).

We selected four factors to characterise food sources: (1) total amino acid concentration, (2) total sugar concentration, (3) amino acid profiles using ordination by nonmetric multidimensional scaling (NMDS) based on Sörensen's similarity index (only accounting for presence or absence of amino acids); two NMDS dimensions were selected as factors (3a) and (3b), (4) sugar 'invertedness' as the concentration ratio (glucose + fructose) / (glucose + fructose + sucrose) (these were the only three sugars in most sources, thus preventing suitable multivariate ordination). Prior to factor selection, Pearson's correlation tests between nectar characteristics from all plant individuals were used to remove redundant factors. This led us to remove the total amino acid : total sugar concentration ratio, the number of amino acids, and per cent sucrose, glucose and fructose concentration from the following analyses, since they were highly correlated with either (1), (3a) or (4), respectively (each $r > 0.69$, $p < 0.01$). Remaining intercorrelations were small (each $r < 0.39$, some $p < 0.01$) except between (3a) and (4) ($r = 0.48$, $p < 0.01$).

Discriminant analysis (DA) was performed to model the contribution of nectar characteristics (1) to (4) to variablity between different groups (individual samples, food sources, and food types). Factors were excluded stepwise forward from each model where $F < 2$.

Software packages used were Statistica 5.5 (StatSoft, Tulsa, USA) for DA and all standard statistical tests, and Community Analysis Package 2.04 for NMDS (Pisces, Lymington, UK).

Results

Resource types and ant visitation

Ant food sources included extrafloral and floral nectar, wound sap and honeydew (Table 1). *Normanbya normanbyi* palms had three potential sources on male inflorescences: nectar from the flower base, large nectar droplet on the sterile pistil, and wound secretions on the inflorescence axis particularly from scars left by abscissed flowers (Fig. 1a). On these palms, wounds were the most attractive sources, flower base nectar was only occasionally consumed, and pistil nectar was never found to be attended by ants. Both wound sap and regular flower nectar were consumed by ants on the other two palm species in the study site as well (Table 1). A different type of wound secretions was found on *Cardwellia*

sublimis trees. Young foliage of these large canopy trees had typically several bitemarks or areas where hairs were shaved along stems, rhachis and leaf midvein (Fig. 1b–1d). These wounds may have been originally caused by herbivorous insects or the ants themselves, but the regular ant activity and the shape of the scratches indicates that ants could be at least responsible for reopening these wounds and prevented their healing. Both types of wound sap use were repeatedly observed on multiple plant individuals during the study. Occasionally, wounds on leaves of *Syzygium sayeri* B.Hyland trees were also attended by ants.

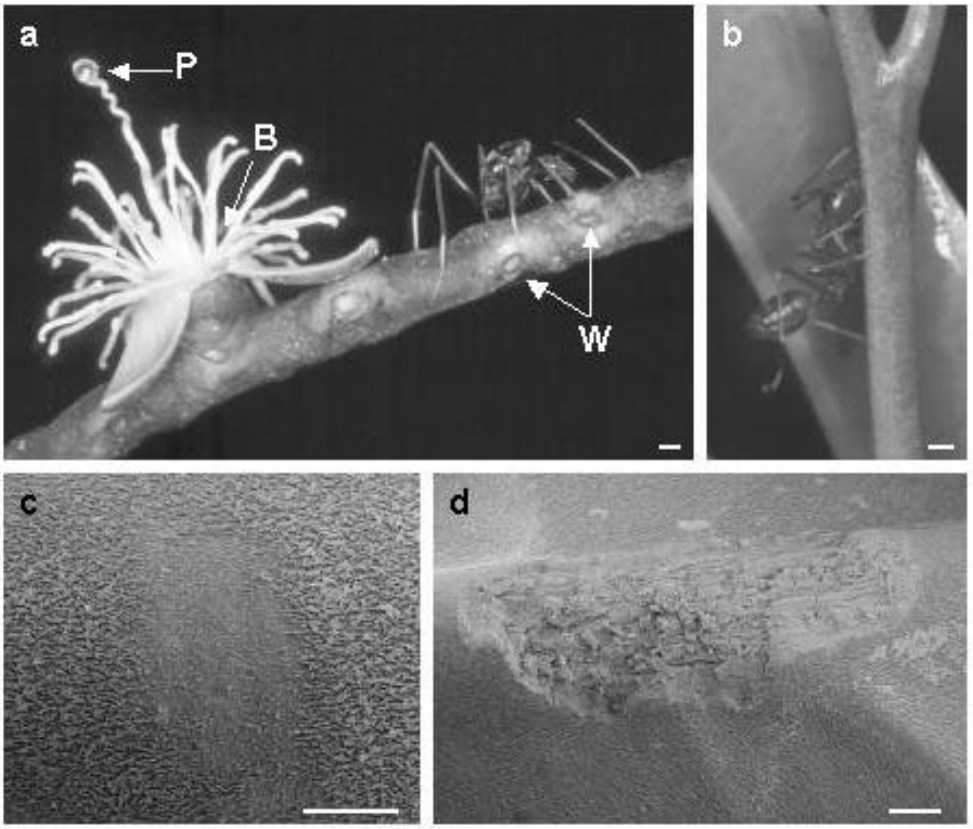

Figure 1 (a-d). Two wound sap sources used by ants in the Australian rainforest. (a) *Normanbya normanbyi* with (P) nectar drop on sterile pistill, (B) flower base nectar and (W) wounds from flower abscission, the latter consumed by a *Leptomyrmex unicolor* ant. (b) *Cardwellia sublimis* twig with *Oecophylla smaragdina* licking sap from a wound that (c) consists of a section with shaved hairs (same twig) or (d) bitemarks that are several tissue layers deep (leaf midvein). Scale bars in (a) and (b) are 1 mm; (c) and (d) are scanning electron micrographs, scale bars 0.5 mm.

All extrafloral nectar sources attracted ants, and no productive honeydew sources (homopteran aggregations) were found that were not ant-attended (see *Chapters 2+5*). However, ants were not observed on all flower nectars although they were often common in the vicinity of the unvisited flowers. Some flower nectars were protected against ants by narrow corolla tubes that were only accessible to the smallest ant species (e.g. *Monomorium floricola* Forel was found in tubular *Dysoxylum mollissimum* flowers) (Table 1). Among the non-tubular flowers with accessible nectars, three sources were not

consumed by ants, including *N. normanbyi* pistil nectar (described above), *Syzygium gustavioides* and *Acmena graveolens*. Feeding trials performed with isolated nectar of these three sources (Fig. 2) showed that the low attractiveness of two sources was maintained outside the flowers: *N. normanbyi* pistil nectar was not consumed at all by *Anonychomyrma gilberti* ants, while the sugar control (5% w/w glucose and fructose solution) received significantly higher attendance (Wilcoxon: $Z = 2.5$, $p = 0.01$, $n = 8$ pairs with ant visits). Ants were observed to probe on the pistil nectar treatment, but then turned away immediately. *S. gustavioides* nectar was also significantly less preferred than the control (13% w/w; $Z = 2.4$, $p = 0.02$, $n = 7$), although some nectar was consumed. However, *A. graveolens* nectar palatability did not differ significantly from the control (21.5% w/w; $Z = 1.7$, $p = 0.09$, $n = 10$). The latter test was repeated with different ants (including six species foraging on the same trunk), and again no differences in palatability were found ($Z = 0.5$, $p = 0.59$, $n = 5$).

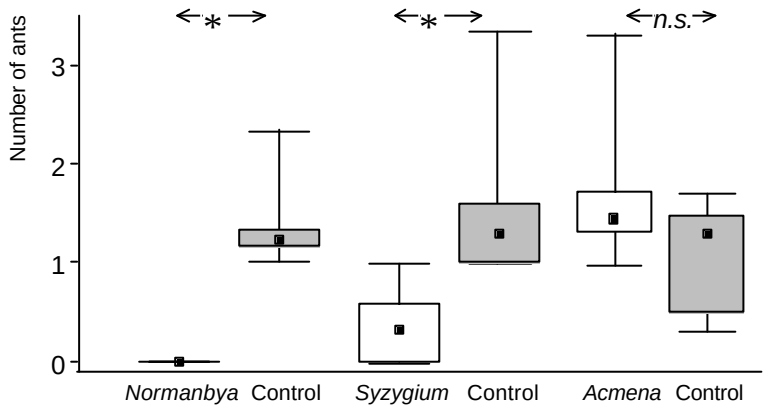

Figure 2. Feeding experiment with untended floral nectar from three sources compared against a control of the same sugar concentration. Boxplots show median, quartiles and range of mean number of ants per tube. Significant differences indicated by an asterisk (*) (Wilcoxon matched pairs).

Table 1 (a-b). Extrafloral and floral nectars, wound sap, honeydew sources, and crop content regurgitated by ants on different sources. Ant attendance or narrow flower tubes indicated by (+). (a) Refractometer and HPLC results of sugar concentration and composition. (b) Amino acid concentration and composition (HPLC). Concentrations of single compounds given as per cent of total weight of identified sugars or amino acids (mean ± SD), a cross (†) marks compounds that did not occur in all samples of a source, compounds that occurred in some samples only as trace amounts (not quantified) were marked by (+), all others by (-). *N* = Number of samples/plant individuals, (n.d.) = no data. Deviation of crop contents from its food source indicated by asterisks (Mann-Whitney U tests, *$p < 0.05$, **$p < 0.01$, *** $p < 0.001$; significances after sequential Bonferroni correction underlined).

Table 1a

Food source		Ants?	Narrow tube?	*N* (Refractom.)	Brix (% w/w)	*N* (HPLC)	Total (g/l)	Fructose	Glucose	Sucrose	Maltose	Lactose	Melibiose	Melizitose	Raffinose
Extrafloral nectar															
Adenia heterophylla (Blume) Koord	Passifloraceae	+		4/1	66±4	2/2	178±68	8±3	7±3	85±7	-	-	-	-	-
Aleurites rockinghamensis (Baill.) P.I.Forster	Euphorbiaceae	+		(n.d.)		2/1	101±59	44	40	17	-	-	-	-	-
Ardisia pachyrrhachis (F.Muell.) F.M.Bailey	Myrsinaceae	+		(n.d.)		5/2	47±41	58±26	34±19†	9±12†	-	-	-	-	-
Clerodendrum tracyanum (F.Muell.) Benth.	Lamiaceae	+		5/1	7±1	3/3	274±366	36±10	39±8	25±18	-	-	-	-	-
Dysoxylum pettigrewianum F.M.Bailey	Meliaceae	+		(n.d.)		5/4	582±320	42±7	46±7	12±13†	-	-	-	-	-
Endospermum myrmecophilum L.S.Sm.	Euphorbiaceae	+		(n.d.)		6/4	187±143	49±7	50±7	1±3†	-	-	-	-	-
Entada phaseoloides Merr.	Fabaceae *s.l.*	+		5/1	41±4	7/5	760±238	21±18†	22±19†	57±37†	-	-	-	-	-
Flagellaria indica L.	Flagellariaceae	+		4/2	32±0	8/5	227±98	16±14†	18±18†	65±34	-	-	-	1±3†	-
Homalanthus novoguineensis (Warb.) K.Schum.	Euphorbiaceae	+		11/2	7±0	4/4	80±18	30±10	29±7	41±17	-	-	-	-	-
Ipomoea indica (Burm.) Merr.	Convolvulaceae	+		2/2	19±6	2/2	215±182	73±38	24±33†	3±4†	-	-	-	-	-
Macaranga involucrata subsp. *mallotoides* (F.Muell.) L.M.Perry	Euphorbiaceae	+		17/5	10±2	4/4	116±44	36±2	36±2	27±4	-	-	-	-	-
Macaranga tanarius Muell. Arg.	Euphorbiaceae	+		14/3	5±2	2/2	70±1	41±5	40±4	19±8	-	-	-	-	-
Mallotus mollissimus (Geiseler) Airy Shaw	Euphorbiaceae	+		2/2	17±15	(n.d.)									
Melicope elleryana (F.Muell.) T.G.Hartley	Rutaceae	+		(n.d.)		1	351	34	24	27	15	-	-	-	-
Merremia peltata Merr.	Convolvulaceae	+		11/2	19±13	11/9	104±50	57±10	41±10	2±2†	-	-	-	-	-
Smilax cf. *australis* R.Br.	Smilacaceae	+		9/2	17±4	3/2	119±8	15±4	7±2†	75±3	-	-	-	4±5†	-
Syzygium erythrocalyx B.P.M.Hyland	Myrtaceae	+		14/4	15±3	5/4	139±102	33±7	33±6	34±13	-	-	-	-	-
Floral nectar															
Amylotheca cf. *dictyophleba* (F. Muell.) Tiegh.	Loranthaceae	-	+	(n.d.)		1	4	100	-	-	-	-	-	-	-
Acmena graveolens L.S. Smith	Myrtaceae	-	-	2/1	25±8	2/1	93±1	23±6	14±1	63±7	-	-	-	-	-
Clerodendrum tracyanum (see above)	Lamiaceae	-	+	13/3	12±3	2/1	150±31	13±1	6±1	81±2	-	-	-	-	-
Cryptocarya hypospodia F.Muell.	Lauraceae	+	-	(n.d.)		2/1	853±40	2±0.2	-	95±2	-	-	-	-	3±2
Cryptocarya murrayi F.Muell.	Lauraceae	+	-	(n.d.)		2/2	547±232	3±1	1±1†	97±2	-	-	-	-	-
Dysoxylum mollissimum subsp. *molle* (Miq.) D.J.Mabberley	Meliaceae	+	+	8/1	15±2	1	233	15	15	70	-	-	-	-	-
Dysoxylum papuanum Mabb.	Meliaceae	+	-	(n.d.)		2/1	409±345	23±6	16±3	61±9	-	-	-	-	-
Elaeocarpus angustifolius Blume	Elaeocarpaceae	+	-	(n.d.)		2/2	169±177	53±0.2	46±1	1±1†	-	-	-	-	-
Embelia caulialata S.T.Reynolds	Myrsinaceae	+	-	(n.d.)		1	930	34	33	33	-	-	-	-	-
Entada phaseoloides (see above)	Fabaceae *s.l.*	+	-	(n.d.)		7/4	361±203	48±7	49±5	4±6†	-	-	-	-	-
Glochidion philippicum (Cav.) C.B.Rob.	Euphorbiaceae	+	-	2/1	20±11	(n.d.)									
Glossocarya hemiderma Benth. & Hook.f.	Lamiaceae	-	+	6/1	17±7	6/2	170±5	26±8	26±7	47±15	-	-	-	-	-
Jasminum didymum G.Forst	Oleaceae	+	-	(n.d.)		1	681	47	53	-	-	-	-	-	-
Liana (identification in progress)	? Rhamnaceae?	+	-	(n.d.)		1	592	28	20	52	-	-	-	-	-
Licuala ramsayi (F.Muell) Domin	Arecaceae	+	-	(n.d.)		3/3	487±639	-	-	100±0	-	-	-	-	-
Normanbya normanbyi (W.Hill) L.H.Bailey (flower base)	Arecaceae	+	-	(n.d.)		1	4	35	-	65	-	-	-	-	-
N. normanbyi (nectar on sterile pistill)	Arecaceae	-	-	8/2	6±0.4	5/5	49±17	14±23	10±20†	76±42†	-	-	-	-	-
Syzygium gustavioides (Bailey) B.P.M.Hyland	Myrtaceae	-	-	6/1	18±22	4/2	167±55	22±5	19±1	59±6	-	-	-	-	-
Viticipremna queenslandica Munir	Lamiaceae	-	+	3/1	35±19	1	203	4	4	93	-	-	-	-	-

Table 1a (continued)

Food source		Ants?	*N* (Refractom.)	Brix (% w/w)	*N* (HPLC)	Total (g/l)	Fructose	Glucose	Sucrose	Maltose	Lactose	Melibiose	Melizitose	Raffinose
Wound sap														
Cardwellia sublimis F. Muell. (bitemarks)	Proteaceae	+	(n.d.)		2/2	986±205	-	-	100±0	-	-	-	-	-
N. normanbyi (scar from flower abscission)	Arecaceae	+	1	18	2/2	162±76	7±5	2±3†	90±2	-	-	-	-	-
Honeydew														
Sextius "kurandae" (Membracidae) on *Caesalpinia traceyi* L. Pedley	Fabaceae *s.l.*	+	(n.d.)		9/3	291±312	11±5†	8±14†	35±28†	3±6†	0.2±0.4†	0.2±0.3†	42±11	-
S. "kurandae" on *E. phaseoloides*	Fabaceae *s.l.*	+	2/1	47±46	11/3	379±527	7±5†	1±2†	65±20	-	-	1±2†	26±12†	-
Milviscutulus sp. (Coccidae) on *Melodinus australis* Pierre	Asclepiadaceae	+	(n.d.)		1	783	14	-	31	-	-	-	55	-
Idiocerinae (Cicadellidae) on *S. erythrocalyx*	Myrtaceae	+	2/1	18±5	5/2	141±135	39±27	5±9†	10±13†	0.4±1†	1±2†	22±24†	-	23±21†
Ant crop content														
Anonychomyrma gilberti Forel on *S. erythrocalyx* (Idiocerinae & EFN)	Myrtaceae	+	5/2	16±5	3/2	81±18	47±3	53±3*	-*	-	-	-	-	-
Leptomyrmex unicolor Emery on *L. ramsayi* flower	Arecaceae	+	(n.d.)		1	891	33	27	-	-	41	-	-	-
L. unicolor on *N. normanbyi* flower	Arecaceae	+	2/1	17±1	4/2	257±23	31±29	26±20*	40±55†	2±3†	-	-	1±2†	-
Oecophylla smaragdina (Fabricius) farming coccoids on *A. graveolens*	Myrtaceae	+	(n.d.)		1	146	25	24	4	7	-	-	5	35
O. smaragdina farming coccoids[1)] on *Endiandra microneura* C.T. White	Lauraceae	+	(n.d.)		1	214	29	24	9	30	-	-	4	4
O. smaragdina farming *Milviscutulus* sp. on *Endiandra* cf. *monothyra*	Lauraceae	+	(n.d.)		1	146	32	30	2	-	6	-	20	10
O. smaragdina farming *Milviscutulus* sp. on *M. peltata*	Convolvulaceae	+	(n.d.)		1	234	30	32	5	-	-	-	20	13
O. smaragdina farming *Sextius "kurandae"* on *C. traceyi*	Fabaceae *s.l.*	+	5/1	16±2	5/4	147±50	30±4**	23±2*	10±8†*	5±7†	-	-	31±4	-
O. smaragdina farming *Sextius "kurandae"* on *E. phaseoloides*	Fabaceae *s.l.*	+	23/2	16±4	7/6	463±428	29±8***	25±11***	13±14**	3±4†**	-	-	31±9	-
O. smaragdina on *Archontophoenix alexandrae* H.Wendl.&Drude flower	Arecaceae	+	(n.d.)		1	51	53	47	-	-	-	-	-	-

[1)] including Coccidae (*Coccus.* sp., *Milviscutulus* sp.) and Ericoccidae

Table 1b

Food source	*N* (HPLC)	Total (g/l)	Alanine	Arginine	Asparagine	Cysteine	Glutamic acid	Glycine	Histidine	Isoleucine	Leucine	Lysine	Methionine	Phenylalanine	Proline	Serine	Threonine	Tyrosine	Valine
Extrafloral nectar																			
A. heterophylla	2/2	4±2	1±1	9±1	-	-	-	0.2±0.3†	31±1	2±1	10±3	2±0	2±1	15±2	8±3	3±0.3	5±1	13±0.4	1±1
A. rockinghamensis	1	3	3	3	-	-	1	-	58	4	3	1	4	4	6	1	2	6	3
A. pachyrrhachis	2/2	0.5±0.3	16±9	-	-	-	-	-	16±23†	4±5†	4±6†	-	-	5±8†	42±50	5±8†	2±3†	5±7†	-
C. tracyanum	2/2	0.3±0.2	25±14	-	-	-	-	-	-	-	-	-	-	-	49±18	-	26±4	-	-
D. pettigrewianum	3/2	1±0.2	24±8	1±2†	-	-	-	-	-	-	-	-	-	-	62±2	-	13±4	-	-
E. myrmecophilum	3/3	2±1	35±20	-	-	-	-	-	-	-	-	-	-	-	57±20	1±2†	3±6†	3±6†	-
E. phaseoloides	5/3	2±0.5	3±4†	9±8†	0.1±0.2†	-	+	0.2±0.3†	+	-	-	-	+	-	78±20	2±2†	8±11†	-	-
F. indica	8/5	11±7	2±2	2±1	0.04±0.1†	4±6†	0.2±0.3†	6±11†	36±16†	4±1	4±1†	1±1†	2±1	10±3	10±8†	8±4	1±1†	7±4	2±1
H. novoguineensis	4/4	0.2±0.1	26±21	1±3†	-	-	-	-	-	-	-	-	-	-	52±20	-	20±6	-	-
I. indica	1	0.3	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-
M. involucrata	4/4	1±0.5	8±10	1±2†	-	-	0.2±0.5†	-	22±15†	0.4±0.4†	2±1†	1±2†	1±1†	8±5†	31±16	6±5†	3±2†	16±5	1±1†
M. tanarius	2/2	0.3±0.04	1±0.1	2±3†	-	-	-	-	-	-	-	-	-	-	73±7	4±6†	19±2	-	-
M. mollisimus	(n.d.)																		
M. elleryana	1	0.4	-	-	-	-	-	-	-	-	-	-	-	-	100	-	-	-	-
M. peltata	11/9	1±1	19±13†	-	-	0.4±1†	1±2†	-	-	-	-	-	-	-	63±17	0.1±0.3†	14±8†	3±6†	-
S. australis	3/2	27±19	6±0.1	6±3	1±1	-	2±0.3	1±0.2	47±6	7±7	5±8†	1±2†	1±0.05	3±4†	1±1	7±1	2±1	7±1	3±0.2
S. erythrocalyx	5/4	0.3±0.1	9±10†	5±6†	-	-	-	-	-	-	-	-	-	-	77±16	0.3±1†	10±12†	-	-
Floral nectar																			
A. dictyophleba	1	0.1	34	-	-	-	-	-	-	-	-	-	-	-	-	29	12	-	26
A. graveolens	2/1	0.3±0.1	5±3	17±5	-	-	-	-	-	-	-	-	-	-	61±5	-	17±2	-	-
C. tracyanum	2/1	0.4±0.1	11±1	15±2	-	-	-	-	-	-	-	-	-	-	52±3	-	22±1	-	-
C. hypospodia	2/1	3±1	2±0.4	7±8	-	-	13±4	-	6±1	-	-	3±4†	-	-	49±7	4±0.2	15±1	-	-
C. murrayi	2/2	4±1	8±0.3	8±1	4±3	9±1	18±0.3	0.3±0.4†	11±1	-	-	3±1	-	3±0.4	21±1	8±2	7±1	-	1±0.4
D. mollissimum	1	1	4	14	-	-	-	-	-	-	-	-	-	-	66	-	15	-	-
D. papuanum	2/1	1±1	7±8	8±11†	-	-	-	-	-	-	-	-	-	-	77±15	-	8±11†	-	-
E. angustifolius	2/2	1±0.5	30±1	-	-	-	-	-	-	-	-	-	-	-	59±0.2	1±1†	10±2	-	-
E. caulialata	(n.d.)																		
E. phaseoloides	7/4	2±1	7±5	1±2†	1±1†	1±2†	1±1†	-	3±4†	1±1†	1±1†	0.4±1†	-	-	63±16	10±8†	9±9†	1±1†	1±1†
G. phillipicum	(n.d.)																		
G. hemiderma	5/2	2±0.2	10±2	6±0.2	-	9±2†	-	-	22±14	2±1†	3±1	-	2±2†	7±1	21±6	6±2	4±3	5±4†	3±0.2
J. didymum	(n.d.)																		
Liana (unidentified)	1	14	24	9	-	-	-	-	6	2	6	-	-	33	6	5	4	4	1
L. ramsayi	1	1	-	17	-	-	-	-	29	-	-	-	-	-	40	-	14	-	-
N. normanbyi base	2/2	0.02±0	62±54	-	-	-	-	-	-	-	-	-	-	38±54†	-	-	-	-	-
N. normanbyi pistill	5/5	0.3±0.2	4±4†	11±6†	-	-	-	-	5±5†	-	1±3†	3±4†	-	6±4†	52±27	3±3†	14±4	-	1±1†
S. gustavioides	4/2	1±0.2	2±1†	5±6†	-	10±17†	5±9†	-	2±4†	+	+	-	-	+	41±12	+	7±4	28±4	+
V. queenslandica	1	2	2	7	-	-	-	-	10	-	-	-	-	50	22	-	10	-	-

Table 1b (continued)

Food source	N (HPLC)	Total (g/l)	Alanine	Arginine	Asparagine	Cysteine	Glutamic acid	Glycine	Histidine	Isoleucine	Leucine	Lysine	Methionine	Phenylalanine	Proline	Serine	Threonine	Tyrosine	Valine
Wound sap																			
C. sublimis	2/2	5±3	10±1	18±3	-	-	-	-	-	-	-	-	-	-	49±8	-	22±6	-	-
N. normanbyi scar	2/2	1±0.2	+	39±5	5±7†	-	17	+	2±4†	-	-	3±4†	+	-	25±4	1±2†	8±4	-	+
Honeydew																			
Sextius/C. traceyi	8/3	7±4	3±2	6±2†	1±1†	0.1±0.1†	2±2†	0.2±0.3†	22±23†	5±1†	6±4†	0.4±1†	0.4±0.4†	8±1†	21±22	6±2†	10±11	5±2†	5±3†
Sextius/E. phaseoloides	12/3	23±45	2±1	6±5	1±1†	10±6†	2±2†	1±2†	19±4†	3±4†	3±3†	3±3†	3±1†	4±1†	17±8	11±5†	10±0.3	4±1†	3±3†
Milv./M. australis	1	2	22	-	-	-	-	-	-	-	-	-	-	-	78	-	-	-	-
Idioc./S. erythrocalyx	5/2	0.2±0.2	6	24±15	-	-	8±31†	+	+	+	+	-	-	4±13†	18±22	+	39±53	-	+
Ant crop content																			
A. gil./S. erythrocalyx	3/2	0.2±0.1	+	-	-	-	-	-	-	+	+	-	-	-	100±0*	+	-	-	-
L. uni./L. ramsayi	1	13	3	20	-	-	-	1	11	3	-	4	-	-	24	25	6	-	2
L. uni./N. normanbyi	4/2	3±3*	2±1	28±3	10±1	-	5±1	0.3±0.3†	8±1*	-	-	4±0.2	3±0.1*	0.3±0.5†	26±15	5±2*	9±4	0.1±0.2†	0.1±0.2†
O. sma./A. graveolens	1	5	3	9	-	1	3	1	13	1	2	3	3	4	34	3	2	15	3
O. sma./E. microneura	1	(n.d.)																	
O. sma./E. monothyra	1	1	2	16	-	-	-	2	8	4	6	2	8	7	26	2	5	5	7
O. sma./M. peltata	1	8	2	13	1	8	4	1	12	3	3	2	4	5	23	7	4	4	5
O. sma./C. traceyi	3/2	5±5	3±2	6±6	0.3±0.4†	-	1±1†	11±16†	18±1†	+	1	-	1±0.5*	12±1	17±19	18±11*	4±2	6±2	3±3
O. sma./E.phaseoloides	7/6	12±12	2±1	5±5	3±4†*	3±6†	6±5†	1±1†	11±3	2±2†	4±2	6±4†	7±6†	7±7†	16±18	12±11†	4±3†*	5±4	6±3
O. sma./A. alexandrae	1	5	5	5	2	3	4	1	17	2	5	4	5	4	27	5	2	4	3

Food source characteristics

Nectar sources showed a high variability in concentration and composition (Table 1). There was no difference between food types in total sugar concentration measured by refractometry (ANOVA: $F_{2, 19} = 0.7$, $p = 0.52$, $n = 22$ food source means). For these measurements, the coefficient of variation (CV) between different nectaries from the same plant individual on the same day was relatively low (mean CV ± SD: 19.9% ± 19.7%, $n = 37$). Variability between means of the same plant individuals measured on different days was similar (mean CV: 23.8% ± 16.3%, $n = 6$). The highest variability was found between plant species (mean CV: 31.7% ± 27.1%, $n = 11$ food sources with multiple individuals), although CVs of these three hierarchical levels did not differ significantly ($F_{2, 51} = 1.4$, $p = 0.27$). Refractometer measures showed a significant linear correlation with total sugar concentrations obtained by HPLC ($r = 0.49$, $p < 0.05$, $n = 20$ food source means), especially for sources with low values (below 20% w/v in both methods: $r = 0.77$, $p < 0.01$, $n = 11$).Sucrose, fructose and glucose were the only sugars found in most nectar and wound sap sources (wound sap is dominated by sucrose). Since sucrose breaks down into glucose and fructose, these two monosaccharides usually occurred in similar concentrations in nectar. In contrast, all four honeydew sources had a broader spectrum of sugars, including the disaccharides maltose, lactose and melibiose, and the trisaccharides melezitose and raffinose. Fructose content largely exceeded glucose in three of the honeydew sources. Three honeydew sources were dominated by melezitose, the other source by raffinose and melibiose. Flower nectar from *Cryptocarya hypospodia* also contained raffinose. Moreover, traces of melezitose were found in EFN from a single *Flagellaria indica* and a single *Smilax* cf. *australis* plant individual, and maltose from a single *Melicope elleryana* plant, but these exceptions may result from pollution or microfaunal activity. Honeydew from membracids feeding on legume vines (*Entada phaseoloides, Caesalpinia traceyi*) had a broad spectrum of amino acids (including all 17 identified amino acids plus many unidentified substances), but some of the EFNs showed a similar range (*F. indica* nectar had the same composition, and in *S. australis* only cysteine was missing).

Food types showed a high overlap in nectar characteristics when all sources were considered (discriminant analysis, Table 2). Extrafloral nectars tended to have a higher relative hexose content than floral nectars, but this difference and variation in other characteristics were not significant (Table 2a). Honeydew and wound sap had higher mean

concentrations of sugars and amino acids than nectar, but again not significantly so (Table 2b, 2c). No significant differences were found between accessible nectar of open flowers and nectar protected by narrow corolla tubes (Table 2d). However, open flower nectar that was regularly harvested by ants had a significantly higher sugar concentration than accessible nectar from the three sources that were not consumed (Table 2e).

Unlike limited variability between food types across all plant species, there were marked differences between food types from the same plant (Table 2f – 2j) and between plant species (Table 2k – 2m). EFN, FN and honeydew occurred simultaneously on *E. phaseoloides* and showed significantly different amino acid profiles between the samples (Table 2f, 2g). Several amino acids were common in membracid honeydew from this liana species but rare or absent from nectar (Table 1). Furthermore, total sugar concentration was higher and relative hexose content lower in EFN than in FN (Table 2f, 2g). *Syzygium erythrocalyx* honeydew secreted by a cicadellid also had a broader spectrum of amino acids but a lower total amino acid concentration than EFN (Table 2h). Of the three sources on *N. normanbyi* inflorescences, wound secretions had the highest, pistil nectar intermediate and basal nectar the lowest total amino acid concentration; these differences were significant (Table 2i, 2j). Pistil nectar had also significantly lower hexose concentration and a few amino acids that were more common.

Interspecific variability was examined for those sources that were represented by multiple

Table 2 (a-k). Stepwise discriminant analysis to model differences in five nectar characteristics (see Methods) between *a priori* defined food types and food sources (EFN: extrafloral nectar, FN: floral nectar, FN_t: nectar from tubular flowers, FN_o: nectar from open flowers, FN_b: nectar from flower base, FN_p: nectar from sterile pistill, H: honeydew, W: wound sap). Significant F-values in bold (*$p < 0.05$, **$p < 0.01$, *** $p < 0.001$). Factors with (-) were not included in the model ($F < 2$).

Model					**Concentration**		**Composition**		
					Amino acids	Sugars	Amino acids		Sugars
	Group 1 : Group 2	*n*	**Whole model**	Factor	(1)	(2)	(3a)	(3b)	(4)
Between food types									
(a)	EFN : FN	32[A]	$F_{1, 30} = 2.0$	$F_{1, 30} =$	(-)	(-)	(-)	(-)	2.0
(b)	(EFN+FN) : H	35[A]	$F_{2, 32} =$ **3.5***	$F_{1, 32} =$	3.7	2.4	(-)	(-)	(-)
(c)	(EFN+FN) : W	34[A]	$F_{1, 32} = 3.5$	$F_{1, 32} =$	(-)	3.5	(-)	(-)	(-)
(d)	FN_t : FN_o	16[A]	$F_{1, 14} = 2.3$	$F_{1, 14} =$	(-)	2.3	(-)	(-)	(-)
(e)	FN_o (ants) : FN_o (no ants)	11[A]	$F_{2, 8} =$ **5.7***	$F_{1, 8} =$	(-)	**10.7***	(-)	5.1	(-)
(f)	*E. phaseoloides* EFN : FN	10[B]	$F_{4, 5} =$ **33.9*****	$F_{1, 5} =$	(-)	**25.1**	**11.5**	**12.9**	**57.0**
(g)	*E. phaseoloides* EFN : H	16[B]	$F_{2, 13} =$ **13.4*****	$F_{1, 13} =$	(-)	(-)	**18.4**	**10.0**	(-)
(h)	*S. "erythrocalyx"* EFN : H	9[B]	$F_{5, 3} =$ **7.1***	$F_{1, 6} =$	**7.8**	(-)	**6.5**	(-)	(-)
(i)	*N. normanbyi* (FN_b+W) : FN_p	8[C]	$F_{3, 4} =$ **11.7***	$F_{1, 4} =$	**34.7****	(-)	**20.0***	(-)	**8.1***
(j)	*N. normanbyi* (FN_b+FN_p) : W	8[C]	$F_{1, 6} =$ **53.5*****	$F_{1, 6} =$	**53.5*****	(-)	(-)	(-)	(-)
Between food sources									
(k)	EFN (13 sources)	44[D]	$F_{48, 109} =$ **5.5*****	$F_{12, 28} =$	**4.4*****	**8.7*****	**2.3***	(-)	**4.1****
(l)	FN (5 sources)	15[D]	$F_{12, 21} =$ **6.3*****	$F_{4, 8} =$	**5.1***	(-)	(-)	**6.1***	**11.5****
(m)	H (3 sources)	8[D]	$F_{4, 8} =$ **8.1****	$F_{2, 5} =$	(-)	(-)	**7.4***	2.1	(-)

Sample size based on:
[A] food source means; [B] samples (incl. replicates from same source plant individuals); [C] source plant individuals; [D] source plant individuals (only food source species represented by two or more individuals).

individuals in this study: First, interspecific differences between EFN sources were significant in all nectar characteristics (Table 2k). Secondly, significant variability between FN sources was found for total amino acid concentration, amino acid and sugar composition (Table 2l). Thrirdly, honeydew from membracids or cicadellids varied only in amino acid composition between three host plant species (Table 2m).

Ant crop analyses

Ant crop contents closely resembled their respective food sources that have been actually visited (Table 1). No significant differences in total sugar and amino acid concentration were found between *Oecophylla smaragdina* and its honeydew sources, and between *Anonychomyrma gilberti* crops and honeydew and EFN of its *S. erythrocalyx* host tree (Mann-Whitney U tests, see Table 1). Sucrose content in crops was reduced and hexoses significantly increased, providing evidence for enzymatic activity (invertase). *A. gilberti* crops contained no sucrose at all and none of the other disaccharides and raffinose found in its honeydew source. *O. smaragdina* crops from trophobioses on *E. phaseoloides* and *C. traceyi* contained the same sugars including maltose that was not found on the former host, indicating that honeydew from different plants may be mixed in crops of the same ant worker. Very few single amino acids deviated significantly from the food sources, none of them significantly so after Bonferroni correction. In contrast, *Leptomyrmex unicolor* crops showed a higher amino acid concentration and significantly higher relative histidine and serine content than nectar and wound sap from palm flowers visited by these ants. In addition, some compounds occurred in some *L. unicolor* crop samples but in none of the palm sources (e.g. lactose, maltose, melezitose) or only in trace amounts (methionine). These could be remnants of resources collected by these ants prior to collection of palm nectar, possibly including insect haemolymph from predation. Of the three sources offered by *N. normanbyi* palms, amino acid profiles of *L. unicolor* crops were most similar to wound sap.

Discussion

Ants used nearly all available sources of plant exudates except for flower nectars of some plant species. Aside from the ‘classical’ ant resources extrafloral nectar and honeydew, floral nectar and wound sap may have been largely underestimated in their significance for ant nutrition (Tobin 1994). Exudates from bitemarks in *Cardwellia sublimis* trees were a rich substitute for nectar, where ants were found to play an active role in damaging plant

tissue. Moreover, wounds on palm inflorescences (*Normanbya normanbyi*) were a very important source, also confirmed by ant crop contents on these palms. Sieve tube sap from palm inflorescences is known as nutrient-rich and is therefore collected by humans (Van Die 1974). In general, different food types (nectar, honeydew, wounds) overlapped in their concentration and composition except for broader sugar profiles in honeydew. Sugars other than sucrose, glucose and fructose were common in honeydew but rare (although occasionally present) in nectar (see also Percival 1961, Beattie 1985, Völkl et al. 1999). Melezitose may dominate some honeydew sources in our study, and elsewhere it has been suggested to play a role as ant attractant (Völkl et al. 1999) or parasitoid repellent (Wäckers 2000). Some honeydews also contain a broad spectrum and high concentrations of amino acids (see also Beattie 1985, Douglas 1993), although some nectars in our study had a similar quality (*Flagellaria indica*, *Smilax* cf. *australis*). Aggregations of honeydew-producing homopterans are typically monopolised by territorial ants. At our study site, ant-homopteran interactions were relatively specialised and only involved a limited subset of the ant community. In contrast, ant-nectar interactions are usually much more opportunistic and different ant species regularly share the same sources (Schemske 1982, Dejean et al. 1997, Blüthgen et al. 2000b). Correspondingly, honeydew sources presented in this paper were monopolised by dominant ants, particularly *Oecophylla smaragdina* (*Chapters 2+5*). The same dominant ant species frequently consumed extrafloral nectar sources that were similar to honeydew with regard to its rich amino acid composition as mentioned above, and those sources were often monopolised in a similar way. Amino acids could thus play a major role in determining the structure of the ant community at liquid food sources.

Proline was the most abundant amino acid in all food source types. In flower nectar, proline can be particularly enriched by pollen contamination (Gottsberger *et al.* 1984, 1990), but non-floral sources in our study had similarly high concentrations of this amino acid. Alanine and threonine were highly abundant as well and only absent from very few sources. Furthermore, arginine, histidine and serine occurred in more than half of the food sources. Asparagine, glycine and the sulfur-containing cysteine and methionine were the rarest amino acids in our analysis. These frequencies may be typical for extrafloral and floral nectars elsewhere, except that histidine is less common, while cysteine, glycine and valine are very common in other nectars (Baker et al. 1978). All 10 amino acids considered essential for insects may be included in nectar or honeydew (Beattie 1985). While different food types did not differ significantly in nectar characteristics, the strongest variability was detected between plant species or between different food sources on the same plant. The

latter was also reported by Baker et al. (1978) for amino acids in co-occurring floral and extrafloral nectars.

Ant crop analyses indicated that the actually visited resources usually make up most of their content, at least in the honeydew feeding dominant ant species *Oecophylla* and *Anonychomyrma*, although mixtures of different sources may occur to some extent, and palm nectar collecting *Leptomyrmex* showed some additional components. The most obvious changes in sugar composition can be attributed to high invertase activity, while amino acid profiles were largely unchanged and included nearly the whole spectrum of amino acids at least in two species.

The attraction of ants to these food sources may benefit plants, since protection by ants has been well documented and may outweigh costs through nectar or honeydew losses (Schemske 1980, Messina 1981, Oliveira 1997, but see Bach 1991). In contrast, ant pollination services are generally very limited (Beattie et al. 1985). Thus, from the plant's perspective it may be often beneficial to avoid ants as floral visitors which can be accomplished by chemical repellents or mechanical barriers. Narrow flower tubes obviously represent such a barrier to most ants, although closer examination sometimes reveals minute ants that are able to access such nectars. No nectar robbery of ants by biting into flower tubes was observed which can be a common phenomenon elsewhere (Herrera et al. 1984). Nectar that was avoided by ants in three open flower sources did not differ from other nectars in sugar and amino acids except for a relatively low sugar concentration. Therefore, nutrient concentration alone is unlikely to explain the lack of ant feeding, since controls with sugar solutions of the same concentrations were readily consumed. It seems likely that ants are repelled from consumption by other (unknown) substances in these nectars and/or by chemical or mechanical barriers on floral structures (see Willmer & Stone 1997, Adler 2000, Ghazoul 2001). Nectar repellents may be involved in *N. normanbyi* pistill nectar and *A. graveolens* nectar, since both isolated nectars were significantly less consumed than controls. However, ant repellents seem to be the exception rather than the rule at the Australian study site. Overall, and ant visitation patterns as observed in the field (*Chapter 2*) appear to be largely driven by nutrition and taste, mediated through carbohydrates and nitrogenous compounds of liquid food sources.

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Chapter 4 – Trophobioses on *Clerodendrum*

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Abstract

***Aphis clerodendri* Matsumurana is newly recorded from Australia and is known from the Northern Territory, on islands in Torres Strait, and in rainforest in northern Queensland and New South Wales. It induces the formation of leaf pseudogalls on native species of *Clerodendrum* and is commonly attended by ants, which penetrate and may polydomously nest in the galls. Previously known only from the Far East, *A. clerodendri* can now be classified as native to Australia and Australasian in natural distribution. The species is herewith also newly recorded from Papua New Guinea and Vietnam.**

Introduction

The Australian aphid fauna is relatively meagre and largely exotic, only about 20 species being known to be indigenous and not many more to be native and Australasian in natural distribution. The recognition of a native Australian aphid species, in this case, *Aphis clerodendri* Matsumura, and of an interesting plant–aphid–ant association is therefore worthy of note.

Morphologically, *Aphis clerodendri* is a member of the *gossypii* group of *Aphis* Linnaeus and, as far as known, is monoecious on, and host-specific to, species of *Clerodendrum* (Verbenaceae) (Inaizumi 1970). It is known from Japan on *C. trichotomum* and *C. yakushimensis* (Matsumura 1917, Takahashi 1966, Higuchi & Miyazaki 1969), and from Korea (Paik 1972, Yoon & Choi 1974) and China (Zhang & Zhong 1983). Records of the highly polyphagous *A. gossypii* Glover on *Clerodendrum* species in Taiwan (Tao 1965), the Philippines (Calilung 1968) and India (Raychaudhuri et al. 1983) merit investigation of the possibility that they refer to *A. clerodendri*.

Aphis clerodendri is recorded as damaging its host in China (Zhang & Zhong 1983) and is shown to deform its host and associate with ants in Korea (Paik 1972). Otherwise, the species appears to be little known.

Clerodendrum (Verbenaceae) is a species-rich genus of mostly trees and shrubs widely distributed in the warm to tropical regions of Australia (Western Australia, Northern Territory, Queensland, New South Wales), Asia, Africa and Central and South America. Of the 10 Australian species, three are indigenous, the rest variously Australasian in distribution (Munir 1989). Other members are present in Australia as ornamentals, e.g. *C. chinense* in botanic gardens in Cairns and Brisbane (Waterhouse 1993). The extrafloral nectaries of many species are attractive to ants.

This paper newly records *Aphis clerodendri* from Australia, Papua New Guinea and North Vietnam and presents observations on its interaction in Australia with its host plants and with attendant ant species.

Abbreviations used include: al., alatae viviparae; apt., apterae viviparae; ny., nymphs; KLA, K.L. Anderson; GAB, Glenn Bellis; NB, Nico Blüthgen; JFG, J.F. Grimshaw; MHJ, M.H. Julien; BMW, B.M. Waterhouse; NSW, New South Wales; NT, Northern Territory; PNG: Papua New Guinea; QLD, Queensland.

Records are presented sequentially as follows: host plant species (alphabetically); State (clockwise, as NT, QLD, NSW); geocode (north to south); locality; date of collection; collector; notes.

Records of *Aphis clerodendri*

ex *Clerodendrum chinense* var. *simplex,* Honolulu rose, stickbush, [=*C. philippinum*]:
VIETNAM: apt., ny., on leaves, Ao Vua, W. of Hanoi, SW of Son Tay, 28.v.1991, MHJ;
apt., ny., on leaves, Ao Vua-Son Tay road, W. of Hanoi, 28.v.1991, MHJ;
apt., ny., in flower heads, Dan Phuong, between Hanoi and Son Tay, 28.v.1991, MHJ;
apt., al., ny., in flower heads, Tam Dao State Farm, N. of Hanoi on Tam Dao road, 29.v.1991, MHJ;
apt., al., ny., Hai Xuan, Mong Cai, Quang Ninh Province, 26.viii.1991, N. Van Cam.
ex *Clerodendrum chinense* (sterile, with double flowers):
apt., ny., on leaves, Nam Sach, E. of Hanoi, 30.v.1991, MHJ;
apt., ny., on young leaves, Som Bong, Cuc Phong Forest, 31.v.1991, MHJ.
ex *Clerodendrum floribundum,* lolly bush:
NT: apt., ny., in leaf pseudogalls, 11°35'S 131°10'E, Melville Island, 13.vi.2001, GAB;
apt., ny., in leaf pseudogalls, 11°51'S 131°51'E, Poonelli, 12.vi.2001, GAB;
apt., ny., in leaf pseudogalls, 12°30'S 135°48'E, Gapuwiyak, 17.xii.1998, GAB.
QLD: apt., ny., in tight, leaf pseudogalls, 10°11'S 142°20'E, St Paul's Community, Moa Island, Torres Strait, 11.iv.2000, KLA;
apt., ny., in leaf pseudogalls, 10°14'S 142°13'E, Kubin Community, Moa Island, 16.viii.1999, JFG, ants: *Paratrechina vaga* (Forel); 10.iv.2000, BMW, KLA, ants: *Iridomyrmex* sp. *hartmeyeri* Forel group;
apt., al., ny., in leaf pseudogalls, 10°15'S 142°29'E, Nagir Island, Torres Strait, 15.iv.2000, KLA, BMW;
apt., ny., in leaf pseudogalls, 11°58'S 141°58'E, Old Mapoon, Cape York Peninsula, 24.vii.2001, JFG,ants: *Pheidole* sp.
ex *Clerodendrum longiflorum*:
QLD: apt., ny., in leaf pseudogalls, 17°14'S 145°47'E, Goldsborough Valley near Kearneys Falls, 12.viii.2001, NB. Ants: *Pheidole* sp. (Myrmicinae), workers. Predators: Coleoptera: Coccinellidae: Sticholotidinae, larva, unidentified. Parasites: Hymenoptera: larvae, unidentified.

ex *Clerodendrum quadriloculare*, fireworks, stardust bush:
PNG: apt., ny., in tight, leaf-shoot pseudogalls, 9°05'S 143°12', Daru Island, 22.v.2001, JFG. (Daru Island in an off-shore island of PNG in Torres Strait.)
ex *Clerodendrum tomentosum*, hairy clerodendrum:
QLD: apt., al., ny., in leaf pseudogalls, 10°51'S 142°22'E, Seisia, Northern Peninsula area, Cape York Peninsula, 17.v.2001, KLA., ants: *Pheidole* sp. NSW: apt., al., ny., on leaves and in leaf shoot pseudogalls, 34°25'S 150°52'E, Mangerton Park (remnant rainforest), 30.iii.2002–1.iv.2002, M. and J.A. Carver, ants: *Notoncus capitatus* Forel and *Paratrechina* sp. ex *Clerodendrum tracyanum*:
QLD: apt., alata vivipara, ny., in leaf pseudogalls, 16°06'S 145°27'E, Cape Tribulation, Australian Canopy Crane Site, Coconut Beach Resort, Environmental Research Station (Bat House) and adjacent lowland forest areas, 10.xii.1999–18.vi.2001, A pril 2002, NB, ants: *Paratrechina vaga*, *Technomyrmex albipes* (Smith), *Camponotus vitreus* (Smith);
apt., in (spinose) leaf pseudogall, 17°14'S 145°47'E, Goldsborough Valley near Kearneys Falls, 12.viii.2001, NB;
leaf pseudogalls, 17°21'S 145°56'E, 'The Boulders' near Babinda, 12.viii.2001, NB. (Pseudogalls observed but inaccessible and contents not investigated);
apt., ny., near Cow Bay, in undisturbed forest, NB;
apt., ny., in leaf pseudogalls, 17°27'S 145°54'E, Mt Bartle Frere, at base, 12.viii.2001, NB, ants: *Paratrechina vaga*;
exuviae, on wrinkled leaves, 17°40'S 145°40'E, Cooro Lands, 15.vii.1971, (in CSIRO Herbarium, Atherton);
exuviae, on wrinkled leaves, 17°53'S 146°06'E, Mission Beach, 27.vii.1966, (in CSIRO Herbarium, Atherton).
ex *Clerodendrum* sp.:
QLD: apt., ny., in loose, leaf-shoot pseudogalls, 9°55'S 144°03'E, Dawar Island, Torres Strait, July 2002, JFG;
apt., alata vivipara, ny., in tight, leaf-shoot pseudogalls, 9°56'S 144°04'E, Murray Island group, Torres Strait, 20.iii.1991, JFG, ants: *Pheidole* sp..

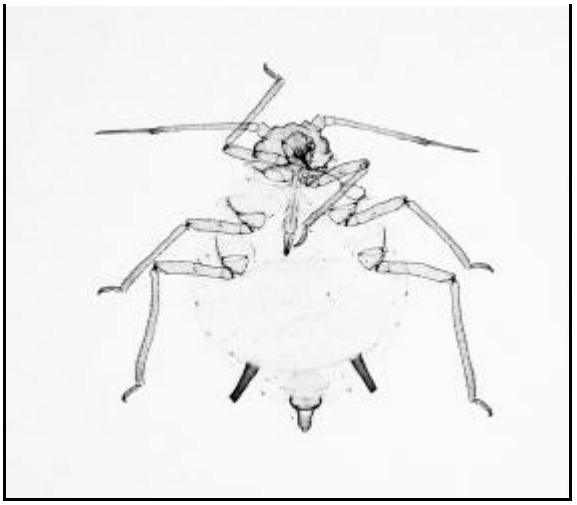

Fig. 1. Aptera vivipara of *Aphis clerodendri* (small, cleared, slide-mounted specimen).

Aphis clerodendri *in Australia*

Aphis clerodendri (Fig.1) was found on *Clerodendrum floribundum, C. longiflorum, C. quadriloculare, C. tomentosum, C. tracyanum* and *Clerodendrum* sp. in the Northern Territory, in the Torres Strait, on Cape York Peninsula, in understory of the Queensland rainforest, where it was especially common, and in remnant rainforest in coastal NSW (above records and Fig. 2). Except in the NSW sample, alatae viviparae were rare and nymphs were mostly apteriform.

Leaf pseudogalls on *Clerodendrum* were very common, especially at Cape Tribulation, where it is estimated that every second *C. tracyanum* was affected. They were observed on both saplings and mature plants, often occurring on several leaves on each plant, including leaf shoots. Where the shoots were galled (e.g. *Clerodendrum floribundum* on Moa Island),

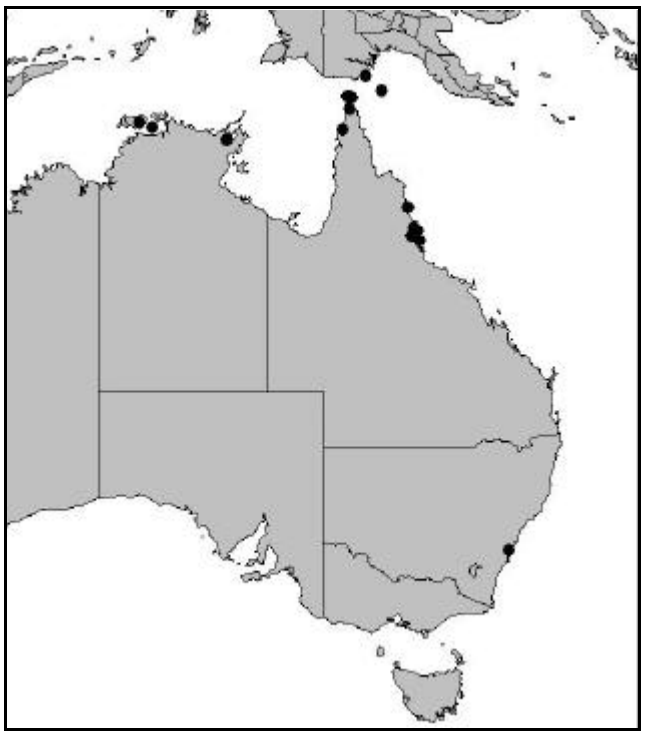

Fig. 2. Known distribution of *Aphis clerodendri* in Australia and New Guinea.

the leaves of the shoots were closed around one another and the leaf tissue was extremely wrinkled, externally giving the appearance of a 'Savoy' cabbage leaf. Internally, the aphids were living in the many nest-like concavities between the veins of the tightly wrinkled (undersurfaces) of the leaves. In the other *Clerodendrum* species where the leaves were older and/or larger, one or two leaves would be curled revolutely to form looser galls (Fig. 3). Early stages of gall formation, in the form of wrinkled, aphid-infested leaves, were also observed. *Aphis clerodendri* was also found on the foliage of *Clerodendrum* in the absence of pseudogalls. 'Fouling' by honeydew was not observed in any of the galls.

Eight or more species of ants were found attending *Aphis clerodendri*: *Iridomyrmex hartmeyeri* Forel group, *Technomyrmex albipes* (Dolichoderinae), *Notoncus capitatus*, *Paratrechina vaga*, *Paratrechina* sp., *Camponotus vitreus* (Formicinae) and *Pheidole* spp. (Myrmicinae). They were commonly present in many galls with *A. clerodendri* in Queensland, including Torres Strait, and NSW, but were not observed in NT. They also attended aphids on the leaves. At Cape Tribulation, both *Paratrechina vaga* and *Technomyrmex albipes* were occasionally found nesting inside the galls, as indicated by the presence of eggs and larvae. They were also observed attending extrafloral nectaries as well as aphids. Nests of both species were common in other cavities of plant structures in this area. On Mt Bartle Frere, larvae as well as workers of *P. vaga* were also found with *A.*

clerodendri within galls. *Camponotus vitreus* was observed on one occasion, at Cape Tribulation, 'stealing' honeydew from a *Technomyrmex*-attended gall.

Natural enemies

A second instar syrphid larva found preying on *Aphis derodendri* in a pseudogall of *Clerodendrum tomentosum* at Mangerton Park, NSW, and reared to adulthood, was identified as *Episyrphus* (*Asiobaccha*) sp. In an unpublished key to Australian Syrphidae produced by F.C. Thompson (1995), it ran confidently to his sp. nov. #88-16. The puparial stage lasted 10 days at room temperature (23°C).

Other predators were found with *A. clerodendri* in galls of *Clerodendrum,* including 2nd instar larvae of an unidentified species of Syrphidae at Seisia and in the Murray Island group, Qld; an unidentified sticholotidine coccinellid larva at Kearneys Falls, Qld, and an adult, scymnine coccinellid *Scymnodes lividigaster* at Poonelli, NT.

Early larval instars of an unidentified hymenopterous parasite were present in most *A. clerodendri* from Kearneys Falls that were dissected.

Fig. 3. Loose leaf pseudogalls of *Clerodendrum tracyanum.*

Aphis clerodendri *in Vietnam*

MH Julien collected the above-listed *Aphis clerodendri* in North Vietnam as part of a search for suitable agents for biological control of *Clerodendrum chinense* in the South Pacific region (Julien 1993). Its biology and interactivity in Vietnam were not investigated; however, the leaves of some of the hosts were observed to be 'crumpled'.

Aphis clerodendri: *Taxonomic notes*

Living specimens: At Cape Tribulation: apterae viviparae: bright yellow-green; At Mangerton Park: apterae viviparae and apteriform nymphs: individually straw coloured to olive green, some nymphs white; alatae viviparae: abdomen green, with light brown, transverse, spinopleural bars on tergites II–III or IV, and VIII.

Specimens newly preserved in ethanol: At Cape Tribulation: apterae viviparae: Body, including head, straw-coloured to light yellow, except for frontal margin which, dorsally and ventrally, is narrowly and diffusely dusky to blackish. Antennal segment I concolorous with body, segment V apically and segment VI dark to blackish, antennae otherwise pale. Ultimate rostral segment black at apex, rostrum otherwise pale. Tibiae dark on apical ¼ to one-fifth, tarsi dark, legs otherwise pale. Siphunculi black. Cauda pale to dusky.

Macerated, slide-mounted specimens (all sites, Australia, *n*=25): Apterae viviparae: Body: length, 1.08–1.43 mm (mean, 1.26); dorsally bearing light, polygonally reticulate ornamentation; body setae short, apically blunt, except for paired setae on abdominal tergite VIII, which are 22–38 µm long; marginal tubercles on prothorax and segments II and VII well developed, small tubercles rarely present singly on segments IV and VI.

Head: frontal area medially developed; dorsally with spinulosely reticulate ornamentation, ventrally spinulosely imbricated; posterior dorsal cephalic setae 7.5–15 µm long.

Antennae 5-segmented or segment III weakly, or rarely completely, divided to form a 6-segmented antenna; 0.52–0.69 (0.63) x body length; processus terminalis 2.42–2.89 (2.70) x its base; and 0.87–1.54 x segment III; basal diameter of segment III 21–24 µm; setae on segment III short, 7.5–12 µm long, apically blunt, usually 3 in number.

Ultimate rostral segment 2.14–2.57 x basal width, and 1.2–1.36 (1.27) x hind tarsal segment 2; bearing 2-3 (2.25) secondary setae.

Legs: dorsal (anterior) setae on hind femora short, 11–19 µm long, first tarsal chaetotaxy: 3:3:2.

Siphunculi 0.15–0.24 (0.2) mm long, 0.10–0.20 (0.16) x body length, 1.32–1.86 (1.54) x caudal length; dark, lightly spinosely imbricated, becoming sparse apicad.

Cauda 0.10–0.15 (0.13) mm long, pale, bearing 4–9 (7) setae, which become stouter and more curved apicad.

Anal plate heterosetose, bearing 10–13 fine and stouter setae.

Genital plate bearing 2–4 anterior setae and 6–11 posterior setae.

Alatae viviparae: antennae 6-segmented.

Macerated, slide-mounted specimens (all sites, Vietnam, *n* = 25): Body length, 1.50–1.78 mm.

Antennal length 0.47–0.51 x body length; length processus terminalis 2.73–2.94 (mean, 2.87) x length its base; setae on segment III, 15 µm long.

Length ultimate rostral segment 1.20–1.21 x length second hind tarsal segment; number of secondary setae, 2–4.

Number of caudal hairs, 8–10 (8.7).

Genital plate bearing 4–6 anterior and 8–9 posterior setae.

The main differences between *Aphis clerodendri* and *A. gossypii* are evidently biological, *A. clerodendri* being specific to *Clerodendrum* and gall-inducing, in contrast to the exceedingly polyphagous nature of *A. gossypii* sens.lat. Morphologically, they differ little. The body coloration of *A.clerodendri* would appear to be variable as in *A. gossypii* but the range of variability is slightly different. Apterae viviparae and apteriform nymphs of *A. clerodendri* may be white, straw-coloured, green, olive green; and the adult cauda is pale to slightly dusky, whereas those of *A. gossypii* may be straw-coloured, pale yellow, 'dirty' green or dull greenish black, often in the same population, and, except in some small specimens, the adult cauda is dusky to very dusky. No other non-overlapping characters were found to separate the two taxa. Except in small specimens, however, the adult cauda of *A. clerodendri* is relatively longer and bears up to 9 setae; that of Australian specimens of *A. gossypii* studied is usually more wedge-shaped and bears up to 6 setae. In addition, 25% of *A. clerodendri* studied bore 3 secondary setae on the ultimate rostral segment; all *A. gossypii* studied from Australia have the usual number for the genus of two. (Descriptions of *Aphis gossypii* may be found in Cottier 1953, Barbagallo 1966.)

The Vietnamese specimens were larger than the Australian. The antennae were also relatively shorter and the average number of caudal hairs higher, differences which may be commensurate with the differences in body size.

Discussion

From its abundant and widespread occurrence in the range of native *Clerodendrum* species and in remote and non-anthropic areas in Australia, we can assume that *Aphis clerodendri* is native to Australia. The observations on the associated antagonists and ants, though limited, are indicative of a natural rather than an exotically derived community. Presumably, what is now a disjunct Australasian distribution of *A. clerodendri* can be attributed to disjunct collector performance.

Ants and galls: The aphid–ant mutualism under consideration is evidently a loose, opportunistic relationship; attendant ants, for example, were not observed in NT and were absent from some galls in Queensland. It is assumed that the ants associate with the aphids in order to obtain honeydew and not or rarely for predatory purposes; observations were possible only of non-galled colonies (the ants became highly disturbed when the galls were opened for investigation).

The importance, if any, of extrafloral nectaries in attracting ants to *Clerodendrum* is not known. Both *Paratrechina vaga* and *Technomyrmex albipes* attended both extrafloral nectaries of *C. tracyanum* and aphids. Both ant species were also found foraging on various other plant species bearing extrafloral nectaries.

Neither *P. vaga* nor *T. albipes* was found in association with any other members of Sternorrhyncha in the study area at Cape Tribulation, despite the fact that species of *Paratrechina* Motschulsky, *Technomyrmex* Mayr and *Pheidole* Westwood are among other common attendant ant species of other aphids, including *Aphis* species, in Australia. Neither of the two common ant species in Queensland rainforests, *Oecophylla smaragdina* (Fabricius) and *Anonychomyrma gilberti* (Forel) was found inside the galls.

The plant–aphid–ant relationship under discussion is not an unusual one: the majority of European *Aphis* species are attended by ants and many of these species also induce the formation of leaf-curl, ‘crumpled nests’, ‘leaf nests’ in their host plants (Stroyan 1984).

Biological control: *Clerodendrum chinense*, Honolulu rose, is a major weed in some Pacific countries, most notably Western and American Samoa, Fiji and Nieu, where it would appear to be a promising candidate for biological control (Waterhouse 1993). Investigation of the feasibility of using *Aphis clerodendri* as a biocontrol agent could be worthwhile.

Acknowledgements
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Chapter 5 – Trophobioses involving *Oecophylla smaragdina*

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Abstract

1. **Tritrophic interactions between the weaver ant *Oecophylla smaragdina* (Fabricius) (Hymenoptera: Formicidae), plants and honeydew-producing trophobionts (Hemiptera: Sternorrhyncha and Auchenorrhyncha, Lepidoptera: Lycaenidae) were studied in a rainforest canopy in Northern Queensland, Australia.**
2. **Most commonly attended trophobionts by *O. smaragdina* at this study site were Coccidae (*Coccus* sp., *Milviscutulus* sp.) and Membracidae (*Sextius* sp.), followed by *Toxoptera aurantii* (Aphidae), *Planococcus citri* (Pseudococcidae), *Icerya* sp. (Margarodidae), an unidentified species of Eriococcidae, *Austrotartessus* sp. (Cicadellidae), and lycaenid butterfly larvae (*Anthene seltuttus*, *Arhopala centaurus* group).**
3. **Most trophobionts were highly polyphagous, and trees and lianas from many plant species and families acted as homopteran hosts. However, lianas were found to play a key role. Firstly, the majority (68%) of aggregation sites was found on lianas, especially on the legumes *Entada phaseoloides* and *Caesalpinia traceyi*, and secondly, per capita ant visitation rate (*VR*) at coccoids was significantly higher on lianas compared to trees. In total, *VR* to homopterans was 64% higher on lianas.**
4. **Sites of ant-homopteran aggregations were regularly replaced by new locations on fresh plant growth. The mean longevity of nests of this polydomous ant species was 131 days, of individual aggregation sites with membracids 54 days and with coccoids 130 days.**
5. **Our results suggest that plant-specific differences in suitability for honeydew-production (especially the availability of lianas) and the availability of preferred trophobionts have a strong influence on the vigour of *Oecophylla* colonies.**

Introduction

Weaver ants of the genus *Oecophylla* are among the most dominant and important ants in tree canopies of the humid tropics of Africa (*O. longinoda* (Latreille)), as well as in South-East Asia, Australia, and western Pacific islands (*O. smaragdina* (Fabricius)). In Australia, the distribution of the latter species is confined to tropical forests or woodlands in the northern and north-eastern parts of the country (Lokkers 1986). *Oecophylla* ants establish huge colonies comprising several tens or hundreds of thousands of workers. Their polydomous colonies cover territories that include the crowns of several trees (Hölldobler 1983, Peng et al. 1998). Weaver-ants use their silk-producing larvae to build nests from leaves spun together (Hölldobler & Wilson 1990). Leaf 'pavilions', where ants and trophobionts are sheltered, but no brood is raised, are constructed in the same way (Way 1963).

Oecophylla colonies play a key role in the ecosystems in which they occur. First, their competitive dominance over many other ant species affects the entire arboreal ant community. *Oecophylla* colonies defend mutually exclusive territories against conspecific colonies or competing ant species, while permitting co-occurrence of certain other ant species (Hölldobler 1983). These territorial patterns in forest or plantation canopies are known as 'ant mosaics' and usually involve a small number of dominant species and a larger number of hierarchically inferior ant species (Majer 1993). Secondly, weaver ants are substantial predators of other arthropods of various sizes (Hölldobler 1983, Dejean 1990), resulting in significant reductions in various insect pests (Australia: Peng et al. 1997; Malaysia: Way & Khoo 1991). Thirdly, trophobiotic interactions between weaver ants and honeydew-producing insects are abundant and diverse. They involve various homopterans and lycaenid butterflies (Way 1963, Hölldobler & Wilson 1990, Fiedler 2001), some of which are specific to weaver ants (Seufert & Fiedler 1996, Eastwood & Fraser 1999). All those effects may potentially translate into increased plant performance as result of reduced herbivory (Messina 1981).

While a strong impact of weaver ants on the canopy flora and fauna seems undisputed, we do not yet know which factors control abundance and distribution of these ants in natural rain forest canopy, and the role of food resources has not been addressed so far. Prey is generally scarce in the rainforest canopy in relation to highly abundant ants (Stork 1991, Floren & Linsenmair 1997), resources derived from plant sap (particularly honeydew) are more abundant and predictable and may explain the success of large arboreal ant colonies with their high energetic demands (Tobin 1994, Davidson 1997, Blüthgen et al. 2000b).

One should therefore expect that composition, abundance and distribution of the herbivorous trophobionts, which in turn may depend on the local flora, will influence the success of *Oecophylla* colonies (bottom-up effects).

Most studies on predation and trophobiosis by weaver ants have been performed in plantations, but the patterns may be substantially different in more complex and species-rich natural ecosystems. The coastal Australian rainforest is characterised by a particularly high abundance of lianas (Tracey 1982). Lianas may therefore play an important role in providing plant-derived sources, such as honeydew or extrafloral nectar, for huge weaver ant colonies. However, their importance to weaver ants has never been addressed explicitly, and is therefore the subject of the current investigation.

The objectives of our study were to:

(1) investigate the effect of plant life forms (trees vs. lianas) and composition of homopteran fauna on the intensity of trophobiosis with *Oecophylla*;

(2) analyse spatial and temporal dynamics of honeydew use by these highly dominant ants; and

(3) compare the host plant specificity of nests and honeydew feeding sites.

Material and Methods

Study site

This study was carried out using the Australian Canopy Crane in Far North Queensland, Australia (16°07' S, 145°27' E, 80 m a.s.l.). The study area contains lowland rainforest 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, and the mean daily temperature is ranging from 22°C (July) to 28°C (January) (Turton et al. 1999). During the study period between September 1999 and May 2001, the forest was in an early stage of recovery from cyclone 'Rona' in February 1999, which damaged large parts of the canopy. The canopy crane was 48.5 m tall, with a jib length of 55 m, which allowed us to directly examine the canopy in a 0.95 ha forest area. Results reported here relate to this area covered by the jib and its immediate surroundings.

Homopterans

Using the canopy crane, homopterans and tending ants were examined on 30 trees with *Oecophylla* nests, including six tree crowns where a complete count was attempted and repeated during different months in order to reveal temporal changes.

'Aggregation sites' (AS) were defined as ant-homopteran sites on a single host plant species which included at least one homopteran and one ant showing characteristic trophobiotic behaviour, and which was separated from the next such spot by at least 20 cm. For each AS, we counted homopteran nymphs and adults greater

than about 1 mm length and ants in their immediate vicinity. We also recorded the host tree or liana species on which homopterans were feeding. Counts at each AS were completed within ca. 3 min. Overall, counts were spread over the period from 8 a.m. to 5 p.m., thus covering much of the daylight hours. Pavilions sheltering homopterans were carefully opened for inspection, but not nests.

The momentary per capita visitation rate (*VR*) was defined for each aggregation site as:

$$VR = \frac{\text{number of ant individuals at the AS}}{\text{number of homopteran individuals at the AS}}$$

Estimates of the number of homopterans on the tree by extrapolation of counts on a few twigs (Blüthgen et al. 2000b, Dejean et al. 2000) were avoided, as variability between branches and between trees and lianas was very pronounced. Due to the relative openness of the canopy in the study plot after the cyclone, large parts of 11 tree crowns were easily accessible for observations, so surveys were regarded as more or less complete. However, numbers of ants and homopterans are only 'snapshots' of the ant colony activity – they neither include ants that have been running between feeding sites and nests during the census, nor do they cover visits of homopterans on adjacent unaccessible trees. Also, diurnal changes in visitation patterns could not be addressed by this means of recording.

Homopterans collected from numerous AS were identified by taxonomic specialists (see Acknowledgements) in order to obtain information about the specificity of their relationship with ants. Because Coccoidea (including Coccidae, Pseudococcidae, Eriococcidae, Margarodidae) were neither collected from all AS nor distinguished in the field, they were pooled and referred to as 'coccoids' in the following analyses.

Dynamics of nests and homopteran aggregations

Oecophylla nests in the study area were recorded in regard to host tree, identity of leaves used, and diameter of the nest [estimated to the nearest 5 cm; 'diameter' in oval nests = (length + width) / 2]. A complete survey of the site was not attempted.

On six trees, locations of active nests and AS were labelled with plastic tape and checked 1–3 times after a time span (*t*) of 19–204 days (*n* = 9 surveys of nest sites vs. 12 surveys of AS).

The mean establishment rate (*E*) and abandonment rate (*A*) of one nest or AS was obtained as:

$E = n / \Sigma$ (number of nests or AS not previously recorded / *t*),

$A = n / \Sigma$ (number of previously active nests or AS that were abandoned / *t*).

Assuming a constant 'mortality' (i.e. proportional abandonment) (*M*) of nests and AS over time, the (more informative) mean longevity of active nests or AS (*L*) was calculated as:

$L = n / \Sigma (M)$

with M = (number of abandoned nests or AS / number of previously active nests or AS) / *t*.

Data analysis

VR was normalised for one-way ANCOVA by log-square-root transformation. Normality of *VR* was confirmed using Kolmogorov-Smirnov tests, and variance homogeneity by Levene tests. Number of homopterans (untransformed) was used as the covariate. For statistical comparison of *VR* between trees and lianas only those trees were considered that carried lianas in the crown, while other tests were performed on all trees. Labelling of the location of AS on six trees showed that only a minority of AS (total 18%) were

identical between different surveys. The high dynamics and the relatively short life span of homopteran nymphs in relation to intervals between surveys led us to pool AS and *VR* from all surveys.

Results

Homopterans

During the entire study, no *Oecophylla* colony was found that did not attend homopterans, and all major trails of this ant in the canopy were lead to aggregation sites with homopterans (AS).

A total of 490 AS was recorded on the 30 trees studied (including repeated censuses on six trees). Most AS involved membracids or coccoids, while associations with aphids, cicadellids, and lycaenids were uncommon (Table 1). The median number of individuals per AS was highest for coccoids (22) and aphids (11), followed by membracids (6), cicadellids (1.5) and lycaenids (1). Mixed aggregations of coccoids and membracids (4 AS), or coccoids and lycaenids (1 AS), were rare. Homopteran species are listed in Table 2 (note that all membracids, aphids, and cicadellids represented a single species each).

Homopteran taxa were very unequally distributed among host plant species and life forms (Table 1). Nearly all AS with membracids (99%) were found on lianas, especially *Entada phaseoloides* and *Caesalpinia traceyi*. In contrast, most coccoids (74% of AS) were consuming sap from trees. The few AS with aphids, cicadellids, and lycaenids were exclusively found on trees. The unequal distribution of AS with coccoids vs. membracids on trees vs. climbing plants was highly significant ($c^2 = 296.1$, $df = 1$, $p < 0.0001$). Many coccoid AS (82 of 188 AS) occurred on trees without suitable lianas in the crown area. Considering only those trees that carried lianas, distribution of coccoid AS across plant growth forms was much more even (61 vs. 45 AS, respectively) and did not significantly deviate from an equal distribution ($c^2 = 1.4$, $df = 1$, $p = 0.24$).

Between 10 and 2115 homopterans (median: 455) were counted on each of 11 tree crowns where we were able to examine most parts of the crown ($n = 26$ surveys). These homopterans were tended by a similar number of *Oecophylla* workers (median: 449, range: 20–1218). Numbers of homopterans and attended ants per tree were significantly correlated (Pearson's $r = 0.79$, $p < 0.001$). Additional coccoids were usually tended inside the nests, but were not counted here since this would have required nest destruction. A closer inspection of a single nest that had been previously abandoned by *Oecophylla*

Table 1. Distribution of aggregation sites (AS) of *Oecophylla smaragdina* tending different homopterans and lycaenids on trees and climbing plants. Data are considered for a total of 30 trees (including eight trees without lianas). Numbers following the tree species correspond to tree labels of the crane site. Cell entries are numbers of AS with the number of investigated tree canopies in brackets. Total numbers of AS and trees are smaller than pooled numbers where different homopterans or food plants co-occurred on the same AS vs. the same tree, respectively. Species of homopterans and lycaenids are listed in Table 2.

Homopteran host plant species [1])	Coccoidea[2])	Membra-cidae	Aphidae	Cica-dellidae	Lycae-nidae [3])	Total
Trees:	*143 (10)*	*3 (2)*	*6 (4)*	*2 (2)*	*3 (3)*	*156 (15)*
Acmena graveolens L.S. Smith (MYRT) #3032	4 (1) M	-	-	-	-	*4 (1)*
Cardwellia sublimis F. Muell. (PROT) #3028 #4025 #5027	11 (3) C	-	-	2 (2)	-	*13 (3)*
Cryptocarya hypospodia F. Muell. (LAUR) #7066	13 (1) Co	-	2 (1)	-	-	*15 (1)*
Endiandra microneura C.T. White (LAUR) #2002	68 (1) C M E	-	1 (1)	-	1 (1) Ar	*69 (1)*
Endiandra cf. *monothyra* B.P.M. Hyland (LAUR) #1004	13 (1) C M	2 (1)	-	-	1 (1)	*16 (1)*
unident. #1023	-	-	1 (1)	-	-	*1 (1)*
unident. #3034	- M	-	2 (1)	-	-	*2 (1)*
unident. #7072	2 (1)	-	-	-	-	*2 (1)*
unident. #7093	1 (1)	-	-	-	-	*1 (1)*
Myristica insipida R.Br. (MYRI) #1059	7 (1) M	1 (1)	-	-	-	*8 (1)*
Synima cordierii Radlk. (SAPI) #7094	-	-	-	-	1 (1) An	*1 (1)*
Syzygium cormiflorum B.P.M. Hyland (MYRT) #5034	19 (1) C M	-	-	-	-	*19 (1)*
Syzygium sayeri B.P.M. Hyland (MYRT) #3023	5 (1)	-	-	-	-	*5 (1)*
Climbing plants:	*49 (15)*	*289 (17)*	-	-	-	*334 (22)*
Lianas: *Caesalpinia traceyi* L. Pedley (CAES)	3 (3) C	196 (4)	-	-	-	*199 (4)*
Entada phaseoloides Merrill (MIMO)	28 (9) C P	90 (13)	-	-	-	*114 (14)*
Merremia peltata Merrill (CONV)	8 (4) M	1 (1)	-	-	-	*9 (4)*
Melodinus australis Pierre (APOC)	5 (1) M	-	-	-	-	*5 (1)*
Stephania japonica Miers (MENI)	1 (1)	-	-	-	-	*1 (1)*
Ficus pantoniana King (MORA)	1 (1) I	-	-	-	-	*1 (1)*
unident.	2 (1)	2 (2)	-	-	-	*4 (3)*
Vines: *Flagellaria indica* Linn. (FLAG)	1 (1)	-	-	-	-	*1 (1)*
Total plants	188 (19)	288 (17)	6 (4)	2 (2)	3 (3)	*490 (30)*

[1]) Plant families: Apocynaceae (APOC), Caesalpiniaceae (CAES), Convolvulaceae (CONV), Flagellariaceae (FLAG), Lauraceae (LAUR), Menispermaceae (MENI), Mimosaceae (MIMO), Moraceae (MORA), Myristicaceae (MYRI), Myrtaceae (MYRT), Sapindaceae (SAPI), Proteaceae (PROT).

[2]) Only partly collected. C = *Coccus* sp. (Coccidae), Co = Coccidae (immature), E = Eriococcidae, M = *Milviscutulus* sp. (Coccidae), P = *Planococcus citri* Risso (Pseudococcidae), I = *Icerya* sp. (Margarodidae)

[3]) Ar = *Arhopala centaurus* group, An = *Anthene seltuttus* (Röber) (lycaenid on #1004 not collected)

revealed 895 scale insects. Numbers of homopterans and ants were highly variable between trees and different surveys (months), although no clear seasonal pattern could be found and ranking of trees was not stable (Figure 1a). It is unclear how much these results were affected by post-cyclone succession. Ants attended homopterans more continuously on lianas throughout the year, while homopteran attendance occasionally dropped to zero on trees (Figure 1b and 1c).

Table 2. Trophobiotic partners of *Oecophylla smaragdina* in this study.

Family	Species
Coccidae	*Coccus* sp.
	Milviscutulus sp.
Eriococcidae	(unident.)
Pseudococcidae	*Planococcus citri* Risso
Margarodidae	*Icerya* sp.
Aphidae	*Toxoptera aurantii* (Boyer de Fonscolombe)
Membracidae	*Sextius* cf. "*kurandae*" [1])
Cicadellidae	*Austrotartessus* sp.
Lycaenidae	*Anthene seltuttus* (Röber)
	Arhopala centaurus group

[1]) Genus in need of revision (Max Day, pers. comm.)

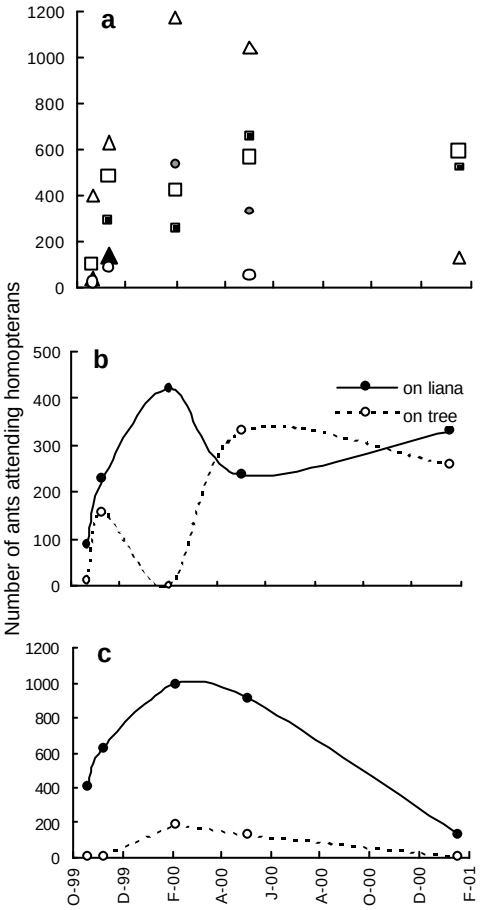

Fig. 1 (a-c). Total number of *Oecophylla smaragdina* workers attending homopterans outside their nests during five surveys between October 1999 and January 2001: (**a**) on six trees incl. lianas (2-5 surveys per tree). Tree numbers (*see* Table 1) are: #1004 (open squares), #2002 (filled squares), #3023 (open circles), #5027 (open triangles), #5034 (filled circles), and #7066 (filled triangles); (**b**) on liana vs. tree as homopteran host plant on #1004 and (**c**) on tree #5027. Smooth curves between the data are plotted for the purpose of readability.

Homopterans varied strongly in aggregation size. There was a significantly higher number of coccoids (mean ±SEM: 59.1 ± 9.2, n = 182) than membracids per AS (10.5 ± 0.9, n = 286) (Mann-Whitney U = 11007, $p < 0.0001$).

Ant visitation rate (*VR*) was negatively correlated with the number of homopterans (H) present at an AS. On a log-log plot (Figure 2), the relationship was linear. The negative

regression was significant for both AS with coccoids (H_c) (log *VR* = -0.22 log H_c + 1.4, r^2 = 0.39, *n* = 174, *p* < 0.0001) and membracids (H_m) (log *VR* = -0.25 log H_m + 1.5, r^2 = 0.23, *n* = 277, *p* < 0.0001). There was no significant difference between the regression slopes for these two homopteran taxa (*t* = 0.84, *df* = 447, *p* = 0.40). These findings lead us to incorporate H as covariate in the following analysis of the effect of plant life form on *VR*, with data from coccoids and membracids combined.

Ant recruitment to trophobionts was significantly affected by host plant life form. Considering only trees that carried lianas, *VR* was 64% higher to homopterans that were feeding sap from lianas compared to trees (Figure 3). This effect was highly significant (ANCOVA: $F_{1, 367}$ = 10.6, SS_{effect} = 0.97, SS_{error}= 0.05, *p* = 0.0016), using H as covariate. The effect on *VR* was slightly weaker, but still highly significant when only coccoids were considered (52% higher on lianas), when all trees were included irrespective of liana presence (45% higher on lianas), or when the covariate was not included.

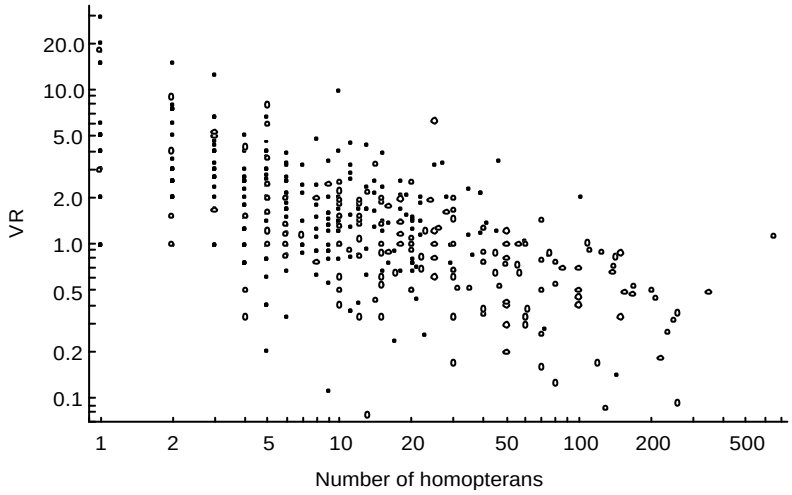

Fig. 2. Relationship between ant visitation rate (*VR*) and total number of homopterans per aggregation site, plotted on log-log scale. Coccoids are represented by open circles, membracids by closed squares.

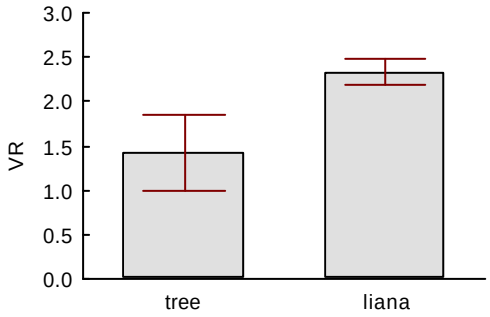

Fig. 3. Visitation rate (*VR* = number of *Oecophylla smaragdina* workers per individual homopteran), compared between lianas vs. trees (where lianas available) as homopteran hosts (mean ± SEM). Mean values vary significantly between plant life-forms (ANCOVA, see text).

Mean *VR* (± SEM) to coccoids on lianas was 1.3 (± 0.2). There was no difference between the two legume species (*Entada phaseoloides* and *Caesalpinia traceyi*) and non-legume lianas (ANCOVA: $F_{1, 35} = 0.33$, $SS_{effect} = 0.01$, $SS_{error} = 0.03$, $p = 0.57$). On two coccoid host trees without lianas (which were excluded from the preceding analysis), *VR* was higher on one tree (*Endiandra microneura*; mean *VR* ± SEM = 2.0 ± 0.3, $n = 68$) and lower on the other (*Cryptocarya hypospodia*, 0.6 ± 0.1, $n = 13$). Among trees with lianas, mean *VR* at coccoids was 1.2 (± 0.4, $n = 19$) on one *Syzygium cormiflorum* and lower on the remaining six trees (mean *VR* ranging between 0.5 and 0.8). Per capita ant recruitment to membracids varied significantly between the legumes *E. phaseoloides* (3.2 ± 0.4, $n = 79$) and *C. traceyi* (2.2 ± 0.1, $n = 191$) (ANCOVA: $F_{1, 267} = 5.3$, $SS_{effect} = 39.6$, $SS_{error} = 7.4$, $p = 0.02$), but was generally higher compared to coccoids.

Locations of *Oecophylla*–homopteran aggregations were highly dynamic. The mean (± SEM) establishment rate of new AS per tree was one AS per 6.8 (± 1.7) days vs. 2.6 (±1.2) days (coccoids vs. membracids, respectively), while one AS per 15.9 (± 5.3) days vs. 3.6 (± 1.2) days was abandoned. Aggregations with coccoids were less dynamic than those with membracids. Mean longevity of AS with coccoids was 130 (± 14) days and only 54 (± 10) days with membracids. The difference in 'mortality' (*M*) of AS with coccids and membracids was significant ($t = 2.6$, $df = 18$, $p < 0.05$; *M* log-square-root transformed).

Oecophylla constructed pavilions with leaves that were woven together with larval silk in a similar way as nests. Number of pavilions per tree varied (mean: 4.6, range 0 – 18, $n = 26$ surveys on 11 trees). Pavilions were usually less than 10 cm in diameter, and therefore considerably smaller than nests of mature colonies. Between one and 15 leaves (median: 3; counted for $n = 59$ AS) were incorporated in each pavilion. They were found on young foliage of trees and lianas where many homopterans were tended by ants, often several meters away from the nearest ant nest. Plants with large leaves or leaflets (> 5 × 5 cm) were more frequently used for pavilion construction (*E. phaseoloides*: 34% of AS; other lianas: 33%, trees: 36%) than *C. traceyi* (15%), a vine with relatively small leaflets (< 2 × 3 cm). Forty-one percent of AS with coccoids and 19% of AS with membracids were sheltered within pavilions. Both factors were interrelated, since most membracids occurred on *C. traceyi* (see Table 1). On one occasion, some ant larvae were found inside the pavilion, which are necessary for the production of silk. Some pavilions were repaired by ants after damage during the census. Pavilions were also abandoned by ants during maturation of the plant tissue in the same way as non-sheltered AS, and mean (± SEM)

longevity was 108 (± 15) days (longer than mean longevity of AS with membracids, similar to AS with coccoids).

Nests

Oecophylla nests were found on 39 trees from over 18 species and eight families of plants (six trees unidentified). Nests were woven from tree or liana leaves (tree leaves only: 24 trees, tree and liana leaves: 11 trees, liana leaves only: four trees). A mixture of tree and liana leaves was used either in separate nests or incorporated in the same nest. The most commonly used liana was *Merremia peltata* (Convolvulaceae). Most common host trees were *Acmena graveolens* and *Syzygium sayeri* (Myrtaceae) (each species represented by four trees inhabited by *Oecophylla*), *Endiandra microneura* (Lauraceae), *Cardwellia sublimis* (Proteaceae), *Argyrodendron peralatum* (Sterculiaceae), and *Myristica insipida* (Myristicaceae) (three trees each). All these common hosts were among the 18 most common and largest trees in the crane plot (each with at least 10 trees of dbh ≥ 10 cm). Sizes of leaves or leaflets utilised by *Oecophylla* were 'normal', ranging from ca. 5 × 8 cm to 20 × 20 cm (upper end: *M. peltata*). The mean height of the 39 *Oecophylla* host trees was 23.2 m (± 1.1 m SEM), and significantly higher than the mean for the remaining trees (15.2 ± 0.2 m, 667 trees of dbh ≥ 10 cm; Mann-Whitney $U = 3429$, $p < 0.0001$). Many examples of common trees that were not recorded as hosts for *Oecophylla* nests were either bearing very large or tough foliage that was obviously unsuitable for nests, e.g. *Alstonia scholaris* R. Br. (Apocynaceae) and palms (*Normanbya normanbyi* L.H. Bailey, *Licuala ramsayi* Domin), or they were relatively small understorey trees (height < 15 m), e.g. *Cleistanthus myrianthus* Kurz (Euphorbiaceae) and *Antirhea tenuifolia* B.D. Jacks (Rubiaceae).

Between one and five nests were found on each tree (median: 3), which were 10–50 cm (median: 30 cm, $n = 34$) in diameter. Nests were frequently abandoned by *Oecophylla* and replaced by new nests. New nests appeared at a rate of one nest per 56 (± 11) days (mean ± SEM), and nests were abandoned at a similar rate (52 ± 11 days). Mean nest longevity was 131 (± 21) days.

Discussion

Sources of honeydew and its use by weaver ants

Our results confirm that for omnivourous weaver ants, apart from preying or scavenging on arthropods and harvesting extrafloral nectar, honeydew derived from various homopteran partners plays a crucial role. Honeydew and nectar may even represent the key resource to compensate the high energy requirements, especially carbohydrate-driven metabolism of adult ants (Davidson 1997) of very large *Oecophylla* colonies in the canopy.

Honeydew production might exceed most floral and extrafloral nectar sources in terms of quantity as well as quality. Indirect evidence supporting this notion comes from the observation that the total number of *Oecophylla* workers tending homopterans was much higher than those tending nectaries at the same time (NB unpublished data). In addition, at our Australian study site a much higher proportion of *Oecophylla* workers returned to their nest with expanded gaster (filled honey-crop) than with prey carried between mandibles (unpublished data). However, these counts could be misleading if hemolymph from insect prey were also carried in the honey-crop (important in red wood ants: Horstmann 1974).

As has been recorded elsewhere (Way 1963), Australian *Oecophylla* ants attend a broad spectrum of homopterans and some lycaenids. Hence, trophobiotic associations are highly unspecific, yet non-random from the ants' perspective. Many lycaenids attended by weaver ants (including the two species found here, *Anthene seltuttus* and one representative of the *Arhopala centaurus* group) are obligate myrmecophiles that associate exclusively with *O. smaragdina* (Eastwood & Fraser 1999). Another potential candidate for an obligate myrmecophile is the membracid *Sextius* cf. *'kurandae'*. *Sextius* species are commonly myrmecophilous (Buckley 1983, Day 1999). Both *Planococcus citri* and *Toxoptera aurantii* are facultative myrmecophiles that may or may not associate with ants (Way 1963, Bigger 1993, Mary Carver, pers. comm.). None of the trophobionts was found with any other ant species in the study area (except some *Icerya* and unidentified coccoids in the understorey). On the other hand, three ant species were very commonly found attending different homopterans that were not attended by *Oecophylla*. Both lycaenid species (Braby 2000) and most homopterans attended by *Oecophylla* in this study are highly polyphagous. Such opportunistic feeding may be a common character of many trophobiotic partners of *Oecophylla* (see Fiedler & Maschwitz 1989). Membracids (*Sextius* cf. *'kurandae'*), scale insects (*Coccus*, *Milviscutulus*), margarodids (*Icerya* sp.), citrus mealybugs (*Planococcus citri*), and aphids (*Toxoptera aurantii*) were each recorded on several host plant families in

this study and/or elsewhere, the latter two species being worldwide pests in plantations (Way 1963, Carver 1978, Bigger 1993, Ben-Dov 1994). The cicadellid *Austrotartessus* was found on two *Cardwellia sublimis* trees, although food plants other than eucalypts and myrmecophily are largely unknown for the entire subfamily Tartessinae (Evans 1981).

Ant-attended homopterans are highly abundant, with a median of 455 homopterans and 449 attending ants per tree in this study. These values are slightly higher than those found in a Venezuelan forest canopy involving 16 ant species (median: 54 membracids or 300 coccoids per tree, Blüthgen et al. 2000b), but considerably smaller than the remarkable values reported by Dejean et al. (2000) from a rainforest canopy in Cameroon ($3 – 7 \times 10^5$ coccoids and the same number of attending *Crematogaster depressa* ants per tree). In *Oecophylla*, a high proportion of coccoids, perhaps even the majority, is attended inside the nest (see also Way 1963).

Nests and homopteran aggregation sites (AS) are highly dynamic and become replaced after a few months. Nests, pavilions, and AS with coccoids had a similarly short durability in this study (108 – 131 days), and AS with membracids were even more short-lived (54 days). The high turnover may be a response to maturation of plant tissue and concomitantly diminishing honeydew productivity or quality (see Douglas 1993), so that fresh tissue is preferably colonised. Membracids are more mobile than largely flightless coccoids in this regard. We did not investigate whether the dynamics of AS can be attributed to replacement (e.g. mortality and predation) of individual homopterans, to their mobility, or to transport by ants. On some occasions however, *Oecophylla* workers were observed to carry *Sextius* nymphs between their mandibles from one AS to another. Transport of trophobionts by *O. smaragdina* and *O. longinoda* is common (Way 1963, Fiedler & Maschwitz 1989).

Pavilions as 'dairies'

The silk-woven pavilions described here (see also Way 1963) are probably analogous to the 'barrack nests' described by Hölldobler (1983) from an area not far from our study site. However, while Hölldobler (1983) suggested that their function was to house guard ants along territorial borders as defence force against intruders, their clustered and temporally restricted distribution on favourable feeding sites for homopterans (young shoots of trees and especially lianas), interspersed between open ant-homopteran aggregations rather than being concentrated along territorial margins or strategically important locations, indicates

their relation with trophobiosis. We therefore conclude that their main use is based on trophobiotic interactions – thus they act as 'dairies' instead of 'barracks'.

Such 'dairies' were also observed in *O. smaragdina* colonies in Malaysia, where they harboured lycaenid caterpillars and membracids (e.g. Fiedler & Maschwitz 1989), and seem to be a common characteristic of these ants. They may be functionally analogous to pavilions built by other ants using silk, debris or carton (e.g. Blüthgen et al. 2000b, Maschwitz et al. 1985, Liefke et al. 1998). All these structures may protect trophobionts and ants against rain and other environmental influences, as well as against competitors or parasites (Way 1963, Gibernau & Dejean 2001).

Trees versus lianas

Weaver ant nests occurred on a broad spectrum of plant species. Many, perhaps the majority of plant species with foliage of normal density and softness, including all common trees or lianas, seem suitable for nest building. Most trees inhabited by *Oecophylla* carried lianas, often with large amounts of foliage in the crown. Some liana species (especially the legumes *E. phaseoloides* and *C. traceyi*) were obviously preferred over trees as feeding ground for ant-tended homopterans. It is difficult to disentangle the effects of life form (lianas) and taxonomy (legumes) in this study, since none of the legume trees (e.g. the common species *Castanospermum australe* A. Cunn. & Fraser) hosted ant-tended homopterans. The preference for legume lianas does not seem to be primarily caused by host plant restrictions on the homopterans involved, since all common homopterans were highly polyphagous.

Instead, we believe that this preference indicates two non-exclusive factors:

(1) A higher quantitative honeydew output of homopterans on lianas. This may be one of the major causes for the higher ant visitation rate to homopterans on lianas compared to trees (including effects within coccoids and a higher *VR* at membracids which are more abundant on lianas).

(2) A higher honeydew quality. Legumes are especially frequent hosts for ant-tended homopterans, possibly as an effect of nitrogen fixation through symbiotic *Rhizobium* bacteria in root nodules. For lycaenid caterpillars in America and Australia, Pierce (1985) found that myrmecophily is particularly common on nitrogen-fixing legumes, although this pattern was challenged by a more detailed analysis (Fiedler 1995).

Lianas may have a more continuous production of new vegetative tissue than trees, which are more seasonal (Putz & Windsor 1987, but see Hegarty 1990). The availability of fresh

tissue for homopterans may be crucial for a high quality and/or quantity of honeydew flow, and thus be often higher on lianas than on trees. Consequently, ant–homopteran interactions in this study were found to be more continuous and intense on lianas than on trees, where they may temporally disappear. The high mobility and turnover of the ant–homopteran aggregations observed in our study may be a potent strategy for maximising honeydew yield by tracking resources in space and time within the ants' territory.

Territoriality in weaver ants may thus be primarily caused by the necessity to maintain a sufficient supply of honeydew. The availability of honeydew may also affect the size of territories: larger territories may be required where the density of high-quality homopteran substrates is low or temporally restricted. The size of *O. smaragdina* territories varies considerably from a single to over 20 major trees (Hölldobler 1983). Territories in the relatively open, liana-rich forest of the study site are restricted typically to relatively few (often 2-3) tree crowns. In South-East Asia, this ant species is much more common in disturbed forests or along forest edges where again lianas are more prevalent (unpublished observations). Forest disturbance through cyclones is not uncommon in northern Australia and is usually followed by rapid regrowth of trees and lianas. The study site represents a typical recovering forest after the severe impact of a cyclone during February 1999. This succession may benefit the nutrition of *Oecophylla* colonies, although immediate short-term impacts of cyclones on *Oecophylla* nests are severe (Begg 1977). We therefore expect that there are close relationships between forest succession, density of homopteran populations, ant territoriality, and territory size, but such conclusions await carefully designed studies, since multiple factors may be involved.

If ants protect trees efficiently against herbivory, the presence of suitable lianas may cause a substantial benefit for the host tree through the attraction of high numbers of resident or visiting ants that indirectly benefit the tree. At the same time, costs of harbouring large numbers of homopterans (loss of phloem sap, risk of infections) are kept to a minimum as long as homopterans preferentially occur on lianas. It would be interesting to investigate whether this pattern could potentially counterbalance costs of liana loads and shading on trees (Stevens 1987) and thus provide a component within the competition between trees and lianas in a forest. Climbing plants (particularly legumes) could also be considered in management of plantations where *Oecophylla* is successfully used as biological control agent (Way & Khoo 1991, Peng et al. 1997), but where plants may be much more susceptible to homopteran-transmitted infections than in natural forest systems, so that the

net effect of ant–homopteran interactions is often viewed as detrimental (James et al. 1997).

Our results emphasize that trophobiotic associations with honeydew producing herbivorous insects are a key component in the foraging of *Oecophylla* ants. There is much variation in the intimacy of relationship towards various honeydew producers. Moreover, trophobiotic aggregations on lianas turned out to be more predictable over the course of the year and received higher per-capita attendance through ants. Due to the predaceous capacity of weaver ants, these patterns have the potential to contribute to ecosystem-wide effects such as the balance between trees and lianas. It remains to be uncovered which characters of honeydew quantity and quality are responsible for the patterns documented here, and how interactions with other ants and nutrient sources contribute to determining spatial and temporal representation of these dominant arboreal ants.

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Chapter 6 – Ant preferences for sugars and amino acids

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Abstract

1. **Feeding preferences of nectarivorous ants for sugars and amino acids were studied in an Australian tropical rainforest using artificial nectar solutions. Fifty-one ant species were recorded feeding on the solutions.**
2. **Preferences among carbohydrates were principally concordant between ant species. In paired tests, sucrose was usually preferred over fructose, glucose, maltose, melezitose, raffinose and xylose, respectively. Occasionally, no preferences were found. Attractiveness of sucrose baits increased with concentration.**
3. **Most common ant species also preferred sugar solutions containing mixtures of amino acids over pure sugar solutions. However, preferences among seven pairs of single amino acids in sugar solutions differed substantially between ant species, including several cases where different ant species displayed significant opposite choices.**
4. **Preferences were significantly reduced when different ant species co-occurred on the same bait. Preferences for single amino acids were also reduced when colonies had extensive access to the same amino acid prior to the experiment.**
5. **Our results indicate that both interspecific variability in gustatory preferences and conditional effects such as competition and colony requirements affect resource selection in multispecies communities. These processes may be crucial in niche partitioning of species-rich nectarivore assemblages.**

Introduction

Niche partitioning is a basic concept in community ecology (Schoener 1974). Within functional groups using the same type of resource, niche partitioning may involve spatio-temporal heterogeneity or other modes of differentiation of resource components. Trade-offs in life-history parameters such as dispersal abilities and non-equilibrium processes like disturbances may promote differentiation and prevent competitive exclusion. These concepts are particularly crucial and controversial in tropical ecosystems where great numbers of species coexist that apparently belong to the same functional group (Novotny et al. 2002, Sheil & Burslem 2003). In the absence of competition, however, niche specialisation may be relaxed. Such conditionality in resource selectivity as a consequence of asymmetric competition has been demonstrated in feeding experiments with three hummingbird species (Pimm et al. 1985).

The functional group of nectarivores is highly diverse in many ecosystems. For floral nectar, flower shapes provide the most obvious feature in association with niche differentiation, e.g. tubular flowers constrain the nectarivore spectrum and promote specialisation (Pyke 1982). Visual and olfactory cues or flowering phenology are other examples, although universal flower/pollinator syndromes may be conceptually too simplified and trends towards specialisation have been over-emphasized in the past (Waser et al. 1996, Ollerton & Cranmer 2002). In extrafloral nectar which is usually presented openly, potentially constraining niche dimensions may be fewer than in flowers, although trichomes and surface structures may limit the visitor spectrum to some extent (Davidson et al. 1989, Federle et al. 2000). Furthermore, honeydew excretions of herbivores may be efficiently exploited only by behaviourally specialised insects that respond to specific cues. One important aspect, however, has been poorly explored so far: the composition of the nectar or honeydew itself may determine preferences of, and partitioning among, nectarivores. Concentration and composition of sugars as the main nutrient component in nectar has been correlated with responses of flower visitors (Percival 1961). Pioneered by Baker and Baker (1973, 1983), amino acids and other substances in nectars have been investigated and certain syndromes have been recognised and related to floral visitors (but see Gottsberger et al. 1984). Studies on actual substance preferences or physiological requirements of nectarivores remain scant (Gardener & Gillman 2002), but provide powerful hypotheses to explain differential resource use. For example, the absence of invertase in some taxa may prevent sucrose digestion and correlate with preferences for monosaccharides (Martínez del Rio 1990). Trisaccharides common in honeydew and

attractive to some insects may be harmful to others (Zoebelein 1956, Wäckers 2000). The uptake rate of sugar solutions may depend on interactions between physical properties and mouth part structures, and trade-offs between viscosity and energy content may occur (Adler 1989, Hainsworth et al. 1991). Physiological requirements of nectarivores may also affect reproductive success as detected for butterflies (O'Brien et al. 2002).

Ants are the most common animals consuming extrafloral nectars and honeydew (Buckley 1987, Koptur 1992), and they may be common on some flowers, although conspicuously absent on others (Janzen 1977), sometimes as a consequence of repellent substances in nectar or floral tissue (Ghazoul 2001). A number of studies have examined sugar preferences of ants (Ricks & Vinson 1970, Sudd & Sudd 1985, Vander Meer et al. 1995, Cornelius et al. 1996, Koptur & Truong 1998, Völkl et al. 1999, Tinti & Nofre 2001). Lanza's work demonstrated that ants prefer some mixtures of sugar and amino acids over others or over pure sugar solutions; mixtures that mimic extrafloral nectar after herbivore attack are particularly attractive (Lanza & Krauss 1984, Lanza 1988, Lanza 1991, Lanza et al. 1993). Most studies have focused on one or two ant species in isolated experimental situations (but see Koptur & Truong 1998, Kay 2002). However, tropical ant communities at natural nectar sources are highly diverse (Schemske 1982) and typically involve many species that co-occur on the same plant (Blüthgen et al. 2000b). Competition between ants can be intense and asymmetrical, resulting in hierarchical communities with superior and inferior species (Fellers 1987, Savolainen & Vepsäläinen 1988). In many tropical sites around the world, the distribution of ant colonies from different species has been described as 'ant mosaics', where dominant species maintain mutually exclusive territories and are associated with a specific assemblage of non-dominant species (Majer 1976b, Jackson 1984b, Majer 1993, Dejean & Corbara 2003). The ant community at our study site was also characterised by an ant mosaic with *Oecophylla smaragdina* and *Anonychomyrma gilberti* as the dominant species and a large set of subordinate species co-occurring with these dominants (*Chapters 2+5*; see also Hölldobler 1983, Majer et al. 2001). However, very little is known about the importance of interspecific competition or resource partitioning in nectar use by ants (Blüthgen et al. 2000b, Hossaert-McKey et al. 2001).

The goal of this study was to examine preferences of ants for sugars and amino acids by experiments with artificial nectar solutions using a multispecies approach in the ants' natural environment. First, we asked whether ant species differ in their preferences and which sugar and amino acid characteristics are subject to interspecific variation. Secondly, we tested whether preferences changed due to previous consumption or through the

presence of competing species. General recruitment, consumption and dial activity patterns of ants and other arthropods observed during this experiment will be presented elsewhere.

Material and Methods

Study site

This study was carried out in Cape Tribulation, Far North Queensland, Australia (16°07' S, 145°27' E, 80 m a.s.l.). Study sites include the Australian Canopy Crane site, the property of the Environmental Research Station and adjacent forest areas. These sites comprise lowland rainforest characterised by a high abundance of lianas and an average canopy height of 25 m (complex mesophyll vine forest, Tracey 1982), secondarily reforested areas and beach forest. Forests were in an early stage of recovery from category 3 cyclone 'Rona' in February 1999 when large parts of the canopy had been severely damaged. 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).

Experimental setup

Sugar and amino acid solutions (ca. 1.7 ml) were offered in standard microcaps (2 ml Eppendorf). The solutions were available to insects through a cotton thread that functioned as a wick (each thread led from the base of the solution to the outside; lids were closed). Wicks outside the lid were ca. 3 cm long and usually quickly soaked with solution near the lid or throughout their entire length. A similar setup was established earlier by Lanza and coworkers (Lanza & Krauss 1984, Lanza 1988, 1991, Lanza et al. 1993). In our experiment, tubes were offered pairwise; each pair was tied together in upright position to a tree trunk at breast height with a plastic tape, wicks were pointing away from the trunk. The order of the two solutions was altered between neighbouring pairs. Selected trees were located at least 8 m apart from each other in order to minimise pseudoreplication by multiple testing of the same ant individuals or colonies.

Two types of experiments were performed:

Experiment-1 was carried out in wide rainforest areas (13.01.–04.03.2001; 01.–06.08.2001). This design attempted to represent a large part of the forest and its characteristic ant community with a minimum of intracolony replication (at the cost of limited sample size for individual species and tests). A total of 663 trees was haphazardly selected along paths regardless of observed ant activity, and only one treatment pair per tree was installed. Paths were used repeatedly for different tests, but time lags between trials at each location were at least one week, and different trees were selected each time. Experimental trials were set up in the afternoon (ca. 15:00–16:00). Ants were subsequently counted at each tube 4–5 times, including afternoon before dusk (ca. 17:00), night (21:00), the following morning (10:00), and afternoon (24h after the start of the experiment).

Experiment-2 aimed to provide a more detailed picture of preferences of colonies from selected species rather than representing the entire community. Experiments included secondary and beach forest besides mature rainforest (20.04.–06.06.2002). A total of 53 trees (separated by ≥ 8 m) was selected on which at least one common target ant species was observed to be active; these trees were repeatedly used for different tests. On each tree, 10 treatment pairs were installed in horizontal and/or vertical rows with at least 10 cm spaces

between pairs. Experiments started at different times during the day; intervals between surveys were at least one hour and at least one survey was performed at night (total 3–5 surveys).

Different mixtures of amino acids or single amino acids were always solved in sugar solutions. Compositions of the sugar-only controls and mixed solutions are given in Table 1. Amino acids in Experiment-1 had constant molarity (total 50 mmol/l amino acids in Mix-A through Mix-D; 100 mmol/l amino acids in Mix-E, Mix-F and all single amino acids). Experiment-2 was based on constant concentration (w/w): total sugars were always 15 g and total amino acids 1 g per 100 g solution in all single or mixed amino acid solutions. Mix-A and Mix-B each contained five amino acids of light and heavy molecular weights in similar proportions, Mix-C was composed of five light and Mix-D of five heavier amino acids. Mix-E contained all 10 amino acids as before, Mix-F was a commercially available product for human muscle training. Mix-G mimicked the amino acid composition of a typical honeydew sample as consumed by ants in the study area (*Chapter 3*). Mix-H was a mixture of the same amino acids as in Mix-G but in equal concentrations. All sugars used were pure D(+)-isomers, except D(-)-fructose and sucrose (commercial white cane sugar). Solutions of trisaccharides (as well as their respective sucrose controls) were presented openly inside the open lids of the tubes, because they were insufficiently dissolved in the threads; these experiments were limited to five hours well before re-crystalisation of trisaccharides became visible.

A pilot study was performed on preferences for 15 synchronously offered amino acid solutions by the two dominant ant species (three colonies of *Anonychomyrma gilberti*, five of *Oecophylla smaragdina*). Pairs of

Table 1. Composition of sugar-only control and mixed amino acid solutions used in preference tests.

		Experiment-1							Experiment-2		
Solution: Substance + Abbrev.		Sugar **mmol/l**	Mix-A	Mix-B	Mix-C	Mix-D	Mix-E	Mix-F [2])	Sucr **mg/g**	Mix-G	Mix-H
Sugars											
Glucose	Gluc	500	500	500	500	500	500	500	-	-	-
Fructose	Fruc	500	500	500	500	500	500	500	-	-	-
Sucrose	Sucr	500	500	500	500	500	500	500	150	150	150
Amino acids [1])											
Alanine	Ala	-	-	10	10	-	10	-		0.3	0.7
Arginine	Arg	-	10	-	-	10	10	6		0.9	0.7
Asparagine	Asn	-	-	10	-	10	10	-		0.1	0.7
Cysteine	Cys	-	-	-	-	-	-	-		-	-
Glutamic Acid	Glu	-	10	-	-	10	10	-		0.5	0.7
Glutamine		-	-	-	-	-	-	8.1		-	-
Glycine	Gly	-	10	-	10	-	10	12		0.1	0.7
Histidine	His	-	-	-	-	-	-	7.4		4.2	0.7
Isoleucine	Ile	-	-	-	-	-	-	7.3		-	-
Leucine	Leu	-	-	10	10	-	10	9.3		0.8	0.7
Lysine	Lys	-	-	-	-	-	-	10		-	-
Methionine	Met	-	10	-	-	10	10	1.2		0.1	0.7
Phenylalanine	Phe	-	-	-	-	-	-	2.6		0.8	0.7
Proline	Pro	-	-	-	-	-	-	-		0.2	0.7
Serine	Ser	-	10	-	10	-	10	-		0.8	0.7
Taurine		-	-	-	-	-	-	8.6		-	-
Threonine	Thr	-	-	-	-	-	-	4.8		0.1	0.7
Tyrosine	Tyr	-	-	10	-	10	10	3.6		0.6	0.7
Valine	Val	-	-	10	10	-	10	7.3		0.7	0.7

[1]) All amino acids offered as pure L-isomers except Met, Phe, Ser and Val (available in mixed DL-form, but only as L-form in Mix-F).

[2]) Commercial powder ("Muscle Gain", Musashi Ltd., Australia); composition as labelled on package; also contains 7.7g glucosamine HCl and 2.6g sugar-based "lemon flavour" per 100g powder.

amino acids in the final experiments were deliberately chosen in order to represent large interspecific variation in preferences as indicated by the preliminary study. For two solution pairs, experiments were repeated after five days for three colonies each of *A. gilberti* and *O. smaragdina* in order to test changes in preferences. Prior to the second experiments, these colonies were given access to large amounts (> 100 ml) of a 4% (w/w) solution of the single amino acids previously preferred in the pairwise tests (serine in the first, leucine in the latter species) for over 48h. Note that all amino acid solutions mentioned before contained sugar like natural nectar sources. Two additional tests were performed using only asparagine or phenylalanine (2% w/w) in water (pairwise tests against water as a control). In addition to tests of variable composition, we tested four concentration levels of sucrose (5%, 20%, 35%, 50% w/w) simultaneously, using the same methods like above except that only five replicates were installed per tree.

Total sugar concentration (°Brix) was checked before and after selected experiments with a handheld refractometer (Eclipse, Bellingham & Stanley). As expected, droplets taken from the threads after the experiment (24h) had a higher sugar concentration than the solution as filled into the vial before the trial, but the increase from initial 15% (w/w) solutions was small (1.4% ± 1.6% (w/w), n = 41) and did not vary significantly between different sugars (sucrose, glucose and fructose, maltose; ANOVA: $F_{2,\ 38} = 1.7$, $p = 0.19$). Furthermore, enzymatic activity on threads (possibly from various sources including ant and microbial activity) may be effective, but had a limited impact on composition during the duration of the experiment. Due to invertase activity, 15% sucrose solutions had a median of 0.3% (w/w) glucose (n = 10; > 2% in two cases) on threads and only 0.1% (w/w) in the vials (n = 5) after the experiment (measured with glucose indicator paper; Glucostix, Bayer).

Data analysis

Ant workers that attended the wick of each solution were counted separately for each ant species (A) and vial pair replicate (V) during each survey (S). Each count on the wick of the first solution was denoted as X_{AVS}, on the second wick as Y_{AVS}, and their difference as $D_{AVS} = Y_{AVS} - X_{AVS}$. The mean number and difference during all valid surveys was obtained (denoted as X_{AV}, Y_{AV} and $D_{AV,}$ respectively). The preference of the ant species (A) for one solution over another was denoted as D_A and obtained as the mean D_{AV} across all n_A vial pair replicates where this ant occurred (thus $df = n_A - 1$). Individual counts (Y_{AVS}, X_{AVS}, D_{AVS}) from surveys where the less attended tube was empty or lacking the wick were excluded prior to analysis (a few wicks were bitten off by various animals).

For each solution pair, two hypotheses were tested: First, does one solution receive greater visitation than the other? This was tested for each ant species and resource combination with sufficient sample size ($n_A \geq 5$) using paired t-tests on all paired X_{AV} vs. Y_{AV}. Secondly, do ant species differ in their preferences? An analysis of covariance (ANCOVA) was applied to detect interspecific variation of D_A between ant species (where $n_A \geq 5$). The mean number of ants per vial pair and survey was taken as covariate to control for variation in absolute recruitment. This method was conservative in all cases (F-values were greater when covariates were not included; data not shown). All statistics were limited to the 23 most common ant species from both experiments (including all species that occurred at least on 10 vial pairs in Experiment-1 or 25 vial pairs in Experiment-2).

Surveys where (1) the respective ant species was the only arthropod species on the respective vial pair were distinguished from (2) cases where different species attended the vial pair simultaneously. Henceforth, these

cases are referred to as single occurrences (1) vs. co-occurrences (2), respectively. For above preferences in Experiment-2 (but not for Experiment-1), each D_{AV} was calculated only from single occurrences. A two-way ANCOVA was performed on differences between D_A from (1) and D_A from (2). This analysis was restricted to solution pairs where preferences of most ant species were largely equivocal; species with odd preferences (different sign of D_A) and the rarely co-occurring *A. gilberti* were excluded from this comparison to avoid a bias through their fixed preference. Like above, the inclusion of the covariate (mean number of ants per vial pair) led to smaller effects.

In order to test changes in preferences during the duration of the experiment, we compared D_{AVS} for the first survey where this ant was present (if this was before the third general survey) with D_{AVS} from the final survey where both vials had remaining solution using paired t-tests. As for changes due to co-occurrence, these tests were restricted to species with equivocal preferences (but including *A. gilberti*) and the same selection of solution pairs.

Statistics were performed using Statistica 5.5 software package (Statsoft Inc., Tulsa). Sequential Bonferroni corrections followed Hochberg's (1988) procedure.

Results

Fifty-one ant species were recorded on the experimental solutions (including three similar nocturnal *Camponotus* species that were not always collected for later identification; these species were pooled in the following analyses). For preference analyses below, the 23 most common ants were selected (Table 2). These focal ant assemblages accounted for 90.8% and 98.5% of all ant visits recorded in Experiment-1 and -2, respectively. Some species were highly abundant and occurred on more than 10% of the experimental trees (*P. platypus*, *C.* 'nocturnal', *P. vaga*). Arthropods other than ants made up only 15.4% vs. 2.8% of the visits (including Aranae, Blattodea, Chilopoda, Coleoptera, Collembola, Diptera, Ensifera, Isopoda and Opiliones).

Sugar and amino acid preferences

Results of amino acid preferences are shown in Figures 1-2, sugar preferences in Figure 3. Among the 23 most common ant species, only the relatively uncommon visits of *P. affinis* were not displayed because of their unusually large variability. This species recruited hundreds of workers to both vials in several cases and covered them completely with soil particles (they showed the same behaviour towards other baits such as fruits and meat placed on the ground).

Table 2. Most common ant species on sugar and amino acid solutions. Ant subfamilies: D = Dolichoderinae, F = Formicinae, M = Myrmicinae, P = Ponerinae. N = number of experimental trees visited.

	Abbrev. (used in Figures)	Sub-family	N
Ants (Formicidae)			
Anonychomyrma gilberti (Forel)	Ano	D	67
Camponotus vitreus (Smith)	Cam_vit	F	22
C. "nocturnal" (3 spp.) [1])	Cam_noc	F	128
C. sp6 (*gasseri* gp.)	Cam_6	F	6
Crematogaster cf. *fusca* Smith	Cre_fus	M	54
C. cf. *pythia* Forel	Cre_pyt	M	20
C. sp3	Cre_3	M	4
Echinopla australis Forel	Ech	F	6
Leptomyrmex unicolor Emery	Lep	D	10
Monomorium floricola Forel	Mon	M	45
Oecophylla smaragdina (Fabricius)	Oec	F	53
Paratrechina vaga (Forel)	Par	F	92
P. minutula (Forel)	Par_min	F	23
Pheidole platypus Crawley	Phe_pla	M	186
P. cf. *athertonensis* Forel	Phe_ath	M	8
Pheidologeton affinis (Jerdon)	Phg	M	10
Polyrhachis foreli Kohout	Pol_for	F	32
Rhoptromyrmex wroughtonii Forel	Rho	M	14
Rhytidoponera spoliata (Emery)	Rhy	P	25
Tapinoma melanocephalum (Fabricius)	Tap	D	37
Technomyrmex albipes (Smith)	Tec	D	67
Tetramorium insolens F.Smith	Tem_ins	M	15
T. validiusculum Emery	Tem_val	M	50

[1]) Includes two species from *C. novae-hollandiae* group and *C.* (*Colobopsis*) *macrocephalus* (Erichson)

Preferences among sugars and amino acids varied between ant species (ANCOVA results in Table 3). In Experiment-1, none of the ant species showed significant choices between sugar solutions with amino acid mixtures of similar molecular weight (Mix-A : Mix-B), or between sugar plus single amino acids vs. sugar only, except for a significant discrimination against asparagine and serine by *P. platypus*. Interspecific variability was not significant in these cases. However, interspecific differences between heavy and light amino acid mixtures (Mix-C : Mix-D) and rich amino acid mixtures (Mix-E, Mix-F) vs. pure sugar solutions were pronounced; the latter two remained significant after sequential Bonferroni correction. Some ants significantly preferred light amino acids over heavy ones and pure sugar over Mix-E (*C.* cf. *fusca*, *P. platypus*) or vice versa (*T. albipes*). The more complex amino acid mixture (Mix-F) was particularly favoured by *O. smaragdina*. In Experiment-2, most species showed a preference for sucrose plus amino acid mixtures over pure sucrose. For the honeydew mimic (Mix-G), several species showed high and significant discrimination in contrast to the non-selective *P.* cf. *athertonensis*. Ant species did not discriminate significantly between the complex honeydew mimic (Mix-G) and the mixture of the same amino acids in equal proportions (Mix-H) (hence both solutions were pooled in the following analyses below). Mix-G was significantly preferred over a solution

of its single most abundant amino acid, histidine, particularly by the same ant species that actually attended the honeydew source that functioned as a model here (*O. smaragdina*). However, *O. smaragdina* did not discriminate between one of its most preferred single amino acids, phenylalanine, and the honeydew mimic (only *C*. cf. *pythia* preferred this latter mixture). Significant interspecific differences with contrary choices of some species were found for all pairs of single amino acids except alanine vs. proline. For example, *O. smaragdina* preferred phenylalanine over asparagine, leucine over glycine, and methionine over valine, while *A. gilberti* showed the opposite preferences for these pairs. The latter species also preferred alanine over proline, histidine over cysteine, and serine over threonine, while *O. smaragdina* did not discriminate significantly between these pairs.

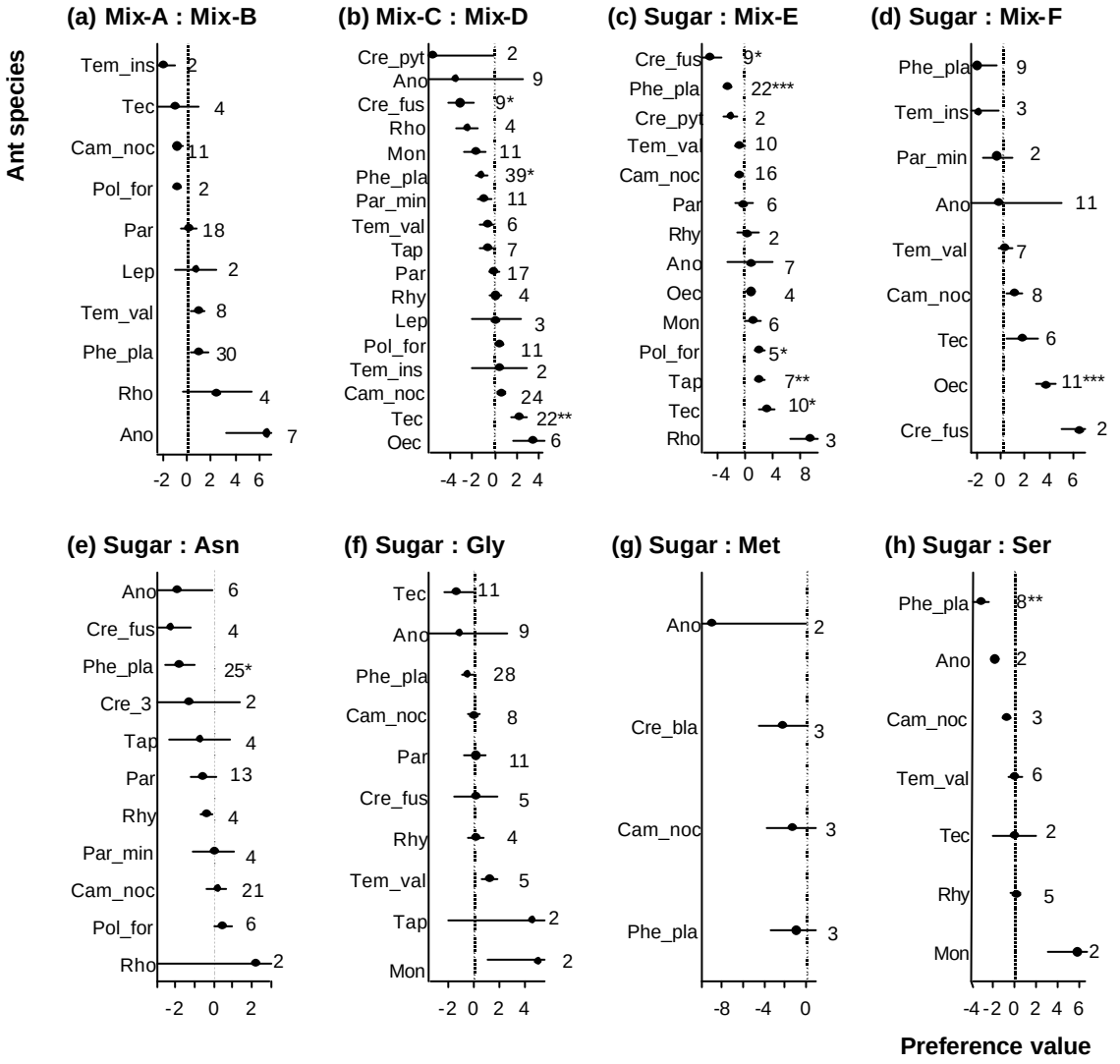

Fig. 1. Amino acid preferences of ant species on broad community level (Experiment-1). Preference values are the mean difference of mean visitation on solution (2) minus that on solution (1). On the left side of the dotted line (indicating no preference), solution (1) is preferred, on the right side solution (2). Composition of solution mixtures given in Table 1 and Methods (amino acids always in addition to sugar). Sample sizes after each bar are number of vial pairs; only those species shown where $n > 1$. Significant preferences indicated by asterisks (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$) according to paired t-tests (applied to all species where $n \geq 5$). Variation between listed ant species with $n \geq 5$ was tested using ANCOVA.

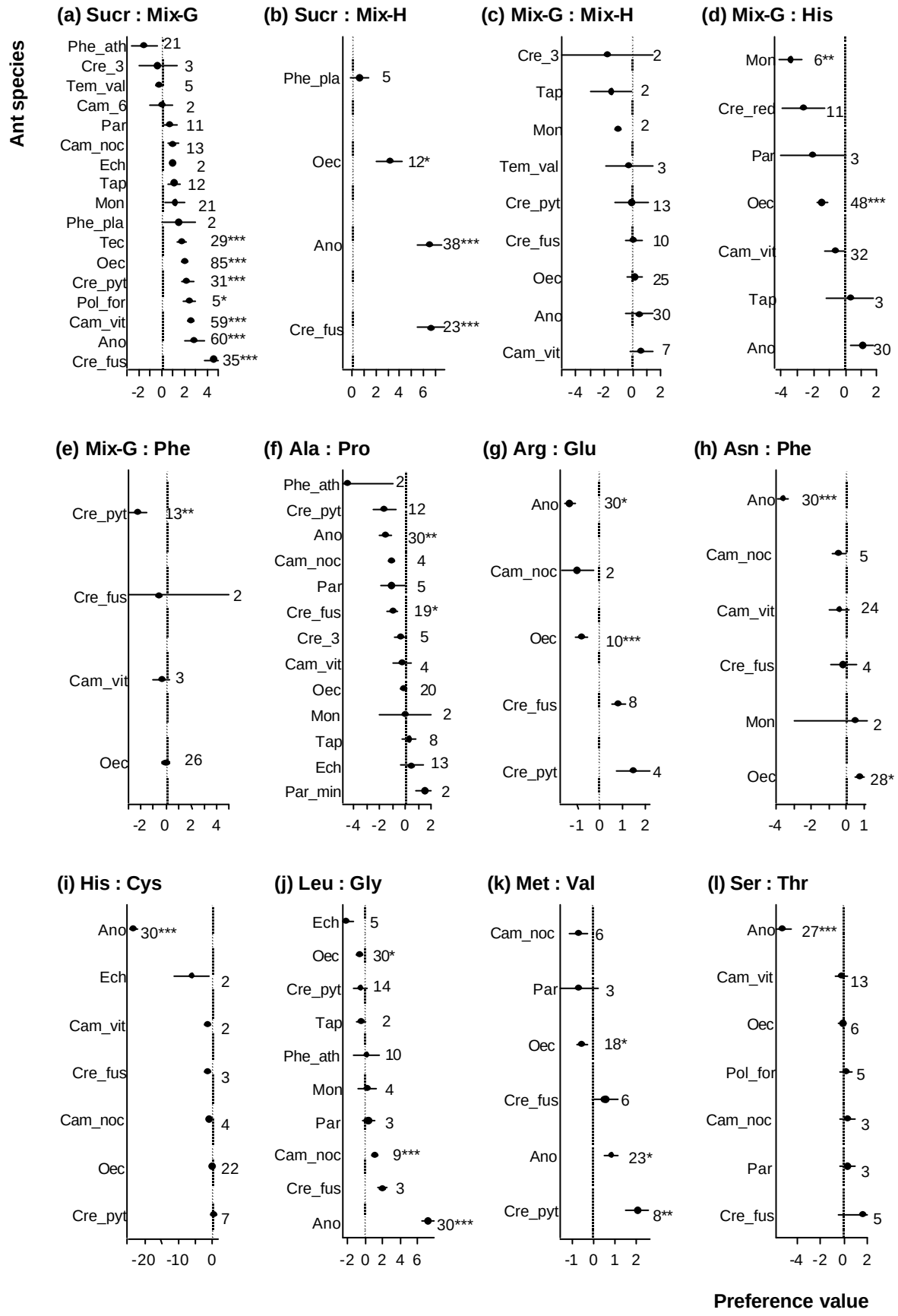

Fig. 2. Amino acid preferences of ant species from selected colonies (Experiment-2). See legend of Figure 1 for details.

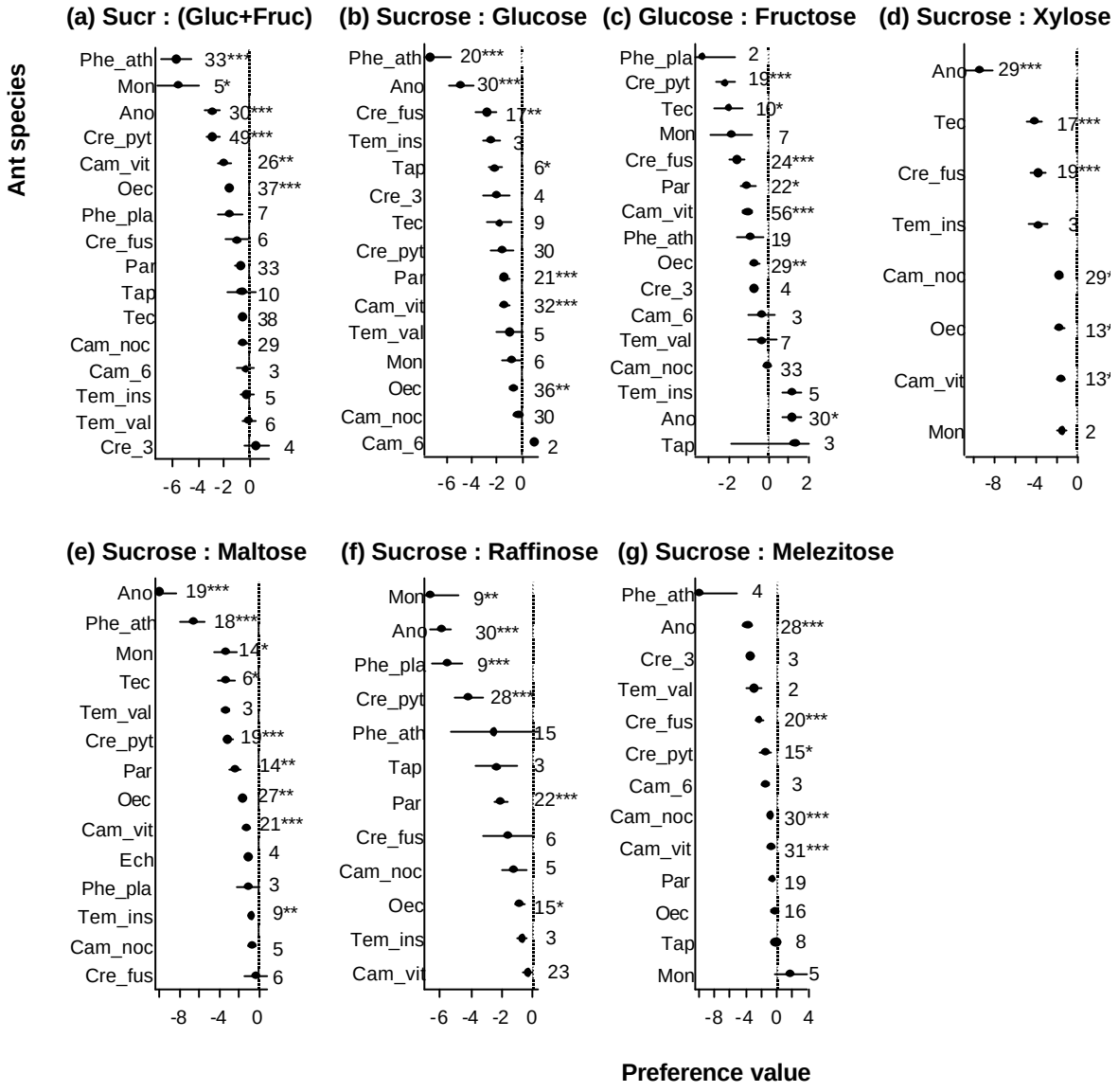

Fig. 3. Sugar preferences of ant species (Experiment-2). See legend of Figure 1 for details.

Ants did not show any preferences for amino acids when offered without sugar. Solutions of asparagine in water were not significantly preferred over pure water (mean ± SEM number of ants; water: 0.5 ± 0.1, Asn: 1.2 ± 0.5, $t_{23} = 1.6$, $p = 0.12$). Furthermore, phenylalanine in water received a similar visitation as the control (water: 0.8 ± 0.1, Phe: 0.8 ± 0.2, $t_{26} = 0.2$, $p = 0.83$). Both amino acids were mainly offered to colonies of ant species that showed a high preference for the same substance when solved in sugar (*O. smaragdina*: Phe; *A. gilberti*: Asn; see Figure 2).

Sugar preferences were similar between most ant species (Figure 3). Sucrose was usually significantly preferred over glucose and fructose, or over glucose alone; few species deviated from this pattern and showed non-significant choices. Glucose was mostly preferred over fructose, although *A. gilberti* had the opposite preference. Xylose was

barely consumed by ants and significantly less attractive than sucrose. The disaccharide maltose and the trisaccharides raffinose and melezitose were significantly less attractive to most ant species, although some species showed no preferences here. Some ants (especially *A. gilberti*) only consumed considerable amounts of melezitose after sucrose controls had been completely emptied.

Ants generally favoured higher sugar concentrations over lower ones; most species showed a consistent increase in visitation with sucrose concentration (Figure 4, incl. all species with $n > 5$). Ant attendance varied significantly between concentrations (ANCOVA, Table 4), and the concentration effect differed between species (significant interaction term). Ants discriminated all four concentration levels offered (Tukey test: all $p < 0.01$), although *Crematogaster* spp. did not differentiate between the highest levels (35% vs. 50%).

Table 3. ANCOVA results for interspecific variation in amino acid and sugar preferences (see Fig. 1-3). Significance levels indicated by asterisks as *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. Significant effects after sequential Bonferroni correction in boldface.

Solution (1) : (2)	*ANCOVA*
Mix-A : Mix-B	$F_{4, 68} = 0.4$
Mix-C : Mix-D	$F_{11, 159} = 2.3$*
Sugar : Mix-E	$F_{9, 87} =$ **4.1*** **
Sugar : Mix-F	$F_{5, 45} =$ **4.6** **
Sugar : Asn	$F_{4, 65} = 1.1$
Sugar : Gly	$F_{6, 69} = 0.5$
Sugar : Ser	$F_{2, 15} = 3.0$
Sucrose : Mix-G	$F_{12, 373} =$ **4.0*** **
Sucrose : Mix-H	$F_{3, 73} = 1.3$
Mix-G : Mix-H	$F_{4, 79} = 0.5$
Mix-G : His	$F_{4, 121} = 1.6$
Mix-G : Phe	$F_{5, 39} = 1.8$
Ala : Pro	$F_{2, 50} = 0.1$
Arg : Glu	$F_{2, 44} = 3.7$*
Asn : Phe	$F_{2, 78} =$ **22.1*** **
His : Cys	$F_{2, 55} =$ **38.1*** **
Leu : Gly	$F_{5, 91} =$ **15.1*** **
Met : Val	$F_{4, 55} =$ **5.5*** **
Ser : Thr	$F_{4, 50} = 2.4$
Sucrose : Gluc+Fruc	$F_{13, 299} =$ **3.5*** **
Sucrose : Glucose	$F_{11, 229} = 1.3$
Glucose : Fructose	$F_{11, 248} =$ **5.8*** **
Sucrose : Xylose	$F_{5, 113} = 1.4$
Sucrose : Maltose	$F_{10, 146} =$ **4.9*** **
Sucrose : Raffinose	$F_{9, 151} = 1.8$
Sucrose : Melezitose	$F_{8, 162} =$ **4.3*** **

Table 4. Two-way repeated measures ANCOVA results for preferences of nine ant species among four sugar concentrations.

Factor	df_{effect}	df_{error}	*F*	*p*
Species	8	181	0.8	0.77
Concentration	3	546	74.3	< 0.0001
Species × concentration	24	546	16.8	< 0.0001

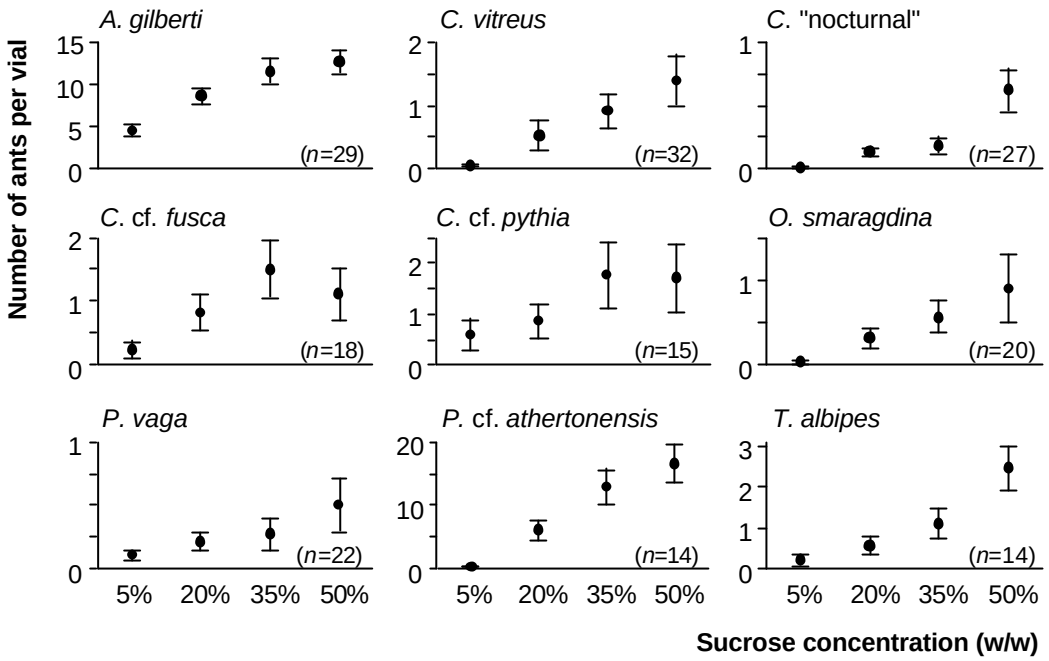

Fig. 4. Visitation of nine ant species among four levels of sucrose concentration (mean number of ants per vial ± SEM).

Conditional changes in preferences

For eight solution pairs, ant preferences were more pronounced during the final survey compared to the first survey where each ant species occurred (paired t-tests, Table 5). However, increases were relatively small for many solutions and only significant for the discrimination against xylose and melezitose after sequential Bonferroni correction. A small and non-significant decrease in sucrose preferences over glucose and fructose was found.

Table 5. Changes in mean preferences between the first and final survey (paired t-tests). Significance levels *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. Significant effects after sequential Bonferroni in boldface.

Solution (1) : (2)	Preferences First : Final	*t-test*
Sucrose : Mix-G/H	2.9 : 4.1	$t_{191} = 2.6$*
Mix-G : His	-0.6 : -1.0	$t_{71} = 0.9$
Mix-G : Phe	-0.5 : -1.2	$t_{36} = 1.9$
Sucrose : Gluc+Fruc	-2.0 : -1.5	$t_{144} = 0.9$
Sucrose : Glucose	-2.8 : -2.7	$t_{128} = 0.2$
Glucose : Fructose	-1.1 : -1.5	$t_{87} = 1.2$
Sucrose : Xylose	-4.7 : -8.7	$t_{42} =$ **3.2****
Sucrose : Maltose	-3.0 : -3.7	$t_{49} = 1.2$
Sucrose : Raffinose	-2.7 : -3.7	$t_{32} = 1.4$
Sucrose : Melezitose	-1.3 : -2.7	$t_{63} =$ **3.4****

Preferences between amino acids changed after ants were fed large amounts of one of the compounds for over two days. *A. gilberti* initially preferred serine over threonine (Figure 2). After access to serine for two days, the direction of the preference remained unchanged, but its extent was significantly reduced (ANCOVA: $F_{1, 48} = 7.6$, $p < 0.01$). Similarly, *O. smaragdina* preferred leucine over glycine (Figure 2); preferences diminished after feeding extensively on leucine, but the effect was only marginally significant ($F_{1, 38} = 3.5$, $p = 0.07$).

The effects of co-occurrence on preferences are displayed in Table 6. The rarely co-occurring *A. gilberti* and those ant species that showed contrary choices from most species were *a priori* excluded from each comparison, and tests did not include solution pairs with highly unequivocal preferences (see Fig. 1-3). In all cases mean preferences decreased when other ant species were present. This trend was significant after Bonferroni correction for preferences between mixed amino acid solutions/sucrose, sucrose/glucose and sucrose/glucose+fructose. The decrease usually affected all species including the dominant *O. smaragdina*. Four species (*C. vitreus*, *C.* cf. *fusca*, *C.* cf. *pythia*, *E. australis*) were commonly associated with *O. smaragdina* (accounting for 215 of 270 co-occurrences with this species). In all solution pairs considered (Table 5, except glucose-fructose and sucrose-xylose with insufficient sample size for these species), mean preferences of the four associates were reduced when they co-occurred with *O. smaragdina*. In turn, preferences of *O. smaragdina* also decreased in five of eight pairs considered, most notably and significantly so in the discrimination between amino acid mixtures (Mix-G or -H) and plain sucrose (mean ± SEM preference for single occurrence $D_1 = 2.1 \pm 0.2$ and co-occurrence $D_2 = 0.9 \pm 0.3$; ANCOVA: $F_{1, 140} = 12.6$, $p < 0.001$).

Table 6. Changes in preferences through simultaneous co-occurrence of different ant species on the same vial pair. Sample size (n) and mean preference (D) ± SEM given for single occurrence (n_1, D_1) and co-occurence (n_2, D_2). Significance levels *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. ANCOVA results in boldface when significant after sequential Bonferroni correction.

Solution (1) : (2)	n_1	n_2	D_1	D_2	*ANCOVA*
Sucrose : Mix-G/H	350	225	2.5 ± 0.2	1.5 ± 0.2	$F_{1, 572}$ = **7.7****
Mix-G : His	105	136	-1.3 ± 0.3	-0.5 ± 0.3	$F_{1, 238}$ = 2.4
Mix-G : Phe	46	50	-0.7 ± 0.3	-0.5 ± 0.3	$F_{1, 93}$ = 0.2
Sucrose : Glucose+Fructose	287	141	-2.0 ± 0.2	-0.5 ± 0.2	$F_{1, 425}$ = **13.0*****
Sucrose : Glucose	220	149	-1.9 ± 0.3	-0.3 ± 0.1	$F_{1, 366}$ = **9.7****
Glucose : Fructose	235	127	-1.0 ± 0.1	-0.5 ± 0.2	$F_{1, 359}$ = 6.8**
Sucrose : Xylose	100	45	-2.7 ± 0.3	-2.2 ± 0.4	$F_{1, 142}$ = 0.6
Sucrose : Maltose	151	67	-2.5 ± 0.3	-1.5 ± 0.5	$F_{1, 215}$ = 6.4*
Sucrose : Raffinose	140	78	-2.5 ± 0.4	-1.2 ± 0.2	$F_{1, 215}$ = 4.2*
Sucrose : Melezitose	154	42	-1.2 ± 0.2	-0.6 ± 0.7	$F_{1, 193}$ = 1.7

Discussion

Sugar preferences

Among the three main nectar sugars, preferences were similar across most ant species (sucrose > glucose > fructose). Few species did not show significant preferences among these sugars, and *Anonychomyrma gilberti* preferred fructose over glucose. Preferences of sucrose over both monosaccharides, variable preferences among glucose and fructose, or non-significant preferences were also reported in other studies on ants (Ricks & Vinson 1970, Vander Meer et al. 1995, Cornelius et al. 1996, Völkl et al. 1999, Tinti & Nofre 2001, but see Koptur & Truong 1998). Invertase is widespread among ants and allows them to digest sucrose (Ayre 1967, Ricks & Vinson 1972). Xylose was not attractive to any of the ants (Vander Meer et al. 1995), and maltose was usually less attractive than sucrose (see also Cornelius et al. 1996, Tinti & Nofre 2001, but Vander Meer et al. 1995). Trisaccharides (raffinose and melezitose) that are common in honeydews in our study site (*Chapter 3*) and elsewhere (Auclair 1963, Völkl et al. 1999) were significantly less attractive than sucrose for most ants, although some species did not show a significant discrimination. For instance, *Oecophylla smaragdina* was equally attracted to sucrose and melezitose, while *A. gilberti* significantly preferred sucrose. Both species commonly fed on honeydew. The most common coccid and membracid honeydew sources of *O. smaragdina* at the study site were dominated by melezitose and sucrose. In contrast, cicadellid honeydew frequently consumed by *A. gilberti* lacked melezitose and was dominated by fructose, raffinose and melibiose (*Chapter 3*). Our findings are not concordant with preferences for melezitose and raffinose over sucrose reported in three studies on European *Lasius niger* ants (Duckett 1974, Völkl et al. 1999, Tinti & Nofre 2001), but they support a study of three tropical ant species where no significant preferences for melezitose over sucrose were found (Cornelius et al. 1996). Melezitose has low phagostimulatory effect or nutritional value to other insects (Wäckers 1999) and can even be toxic (Zoebelein 1956). Besides important osmotic functions for the homopterans, trisaccharides may thus reduce the suitability of honeydew for homopteran parasitoids as host signal or food source (Wäckers 2000). Our results obtained with a broad taxonomic and ecological range of ant species suggest that trisaccharides in honeydew have no general ant-attracting role as proposed earlier (Kiss 1981). Rather some honeydew-foraging ants secondarily evolved the ability to tolerate or assimilate these sugars (e.g. *O. smaragdina*). The ant's enzymatic or microbial equipment could be a constraint on their ability to effectively exploit

honeydew sources, and typically only a fraction of the nectarivorous ant community attends homopteran aggregations (Davidson 1997, Blüthgen et al. 2000b). Apart from behavioural and physiological constraints, however, restricted honeydew foraging may result from active competitive exclusion through territorial dominant ants, since a broad spectrum of nectarivorous ant genera can be at least qualitatively categorised as trophobiotic (see Fiedler 2001). Ant species were similar in their preferences of individual carbohydrates and also consistently preferred higher concentrated sugar solutions over lower ones.

Amino acid preferences

In contrast to carbohydrates, interspecific variability in amino acid preferences was much more pronounced. Most ants preferred solutions containing mixtures of amino acids over sugar alone, with few notable exceptions of contrary or non-preferences (e.g. *Pheidole* or *Crematogaster* species in some cases). These results correspond with previous studies where complex nectar mimics were used (Lanza 1988, 1991), while more simple combinations of amino acids were often less attractive than sugar-only controls (Lanza & Krauss 1984). Species may differ in their preference for amino acid mixtures in the field (Lanza 1988, Lanza et al. 1993) or under laboratory conditions (Lanza 1991). It is not clear if and how discrimination of single amino acids translate into preferences for more complex mixtures. Preferences for some mixtures containing amino acids over sugar-only solutions were more uniform across ant species in our study, suggesting that positive effects of the amino acid mixture outweigh potential repellent functions of some single amino acids (but see Lanza & Krauss 1984). Interestingly, sugars are important in the preference of amino acid solutions, since sugar-free amino acid solutions were not found to be attractive to ants in our study. Other studies also reported that several amino acid solutions without sugar were not accepted by ants (Ricks & Vinson 1970), although such effects may vary between species (see Kay 2002). Synergetic effects between sugars and amino acids may be important and were recently detected for glucose and glycine in the response of ant taste receptors, where the amino acids may enhance the sweetness perception (Wada et al. 2001).

Variability and conditionality

Differences in amino acid preferences may help to explain field observations of nectar and honeydew source partitioning in the ant community (Schemske 1982, Blüthgen et al. 2000b, Apple & Feener 2001, Hossaert-McKey et al. 2001). Multiple factors potentially

cause different dietary preferences in ants, although little is known about their importance. For instance, physiological causes may be distinguished from ecological factors, and both may interact. Physiological factors may involve species-specificity in taste reception or digestive systems (Ayre 1967, Davidson 1997). Ecological variability may be found for energy budgets and nutrient requirements. Since most ants are omnivores and nectar is rarely or never their sole diet (Stradling 1978), the need for nitrogen may vary with the relative importance and complementary composition of other sources. Consequently, ant species that commonly collect nectar and honeydew may exhibit higher preferences for sources rich in proteins or amino acids (Kay 2002) which may reflect the nitrogen limitation of their diet (Yanoviak & Kaspari 2000). Requirements for certain compounds may also vary due to the ants' highly specific chemical communication or defence system (Hölldobler & Wilson 1990). Our results weakly support both physiological constraints and environmental factors, since the degree of preferences between amino acids but not their direction changed after one of the two amino acids had been supplemented in large amounts for two days. During shorter time intervals in the experiments, none of the preferences was altered rather than strengthened, perhaps as a result of experience. Preferences among sugar concentrations and between sucrose vs. amino acid solutions may change according to colony demand and resource availability (Sudd & Sudd 1985, Cassill & Tschinkel 1999, Kay 2002), and our experiments indicate that such processes may even apply to single substances.

Sugar and amino acid preferences were also directly influenced by competition. When other species were absent, preferences of each species were much stronger than in the presence of competitors. Such effects have been demonstrated earlier for hummingbirds on feeders with sucrose solution of different concentration (Pimm et al. 1985) and for choices of ants between fish and syrup baits (Savolainen & Vepsäläinen 1988). Both studies found negative effects in resource selection only for competitively inferior species. In contrast, competition effects in our study were reciprocal on co-occurring species, and affected the dominant *O. smaragdina* as well as its common associates. *O. smaragdina* frequently pinched other ants during the experiment or pulled them away from the solutions, although these interactions were rarely harmful to any of the partners (NB pers. obs.). This behaviour rarely resulted in monopolisation of the solutions by dominant ants, and co-occurrences among *O. smaragdina* and non-dominant ants were relatively common. However, when tuna meat baits were used instead of sugar solutions, *O. smaragdina* aggressively defended and effectively monopolised the baits (NB pers. obs.). Dominance

by competitively superior ant species may be characteristic for meat baits (Fellers 1987, Savolainen & Vepsäläinen 1988). These differences indicate a behavioural shift between high- and low-quality resources. Among poorer resources, competition effects on preferences of dominant and submissive species may be reciprocal. In turn, when quality differences are large (e.g. carbohydrate-based vs. protein-based diets), competitive asymmetries may be more pronounced. Natural honeydew sources and some amino acid rich extrafloral nectars were effectively monopolised by *O. smaragdina* (*Chapter 2+5*), which may be typical for most trophobioses (Blüthgen et al. 2000b). Several factors may explain their higher attractiveness for monopolisation by dominants compared to our experimental solutions (despite their similar composition), including temporal continuity and higher quantity (*Chapter 5*), or spatial scales and architectural features of plant canopies (Hölldobler & Lumsden 1980). Correspondingly, Yanoviak and Kaspari (2000) found that baits in the canopy were significantly more often monopolised than baits on the ground.

In conclusion, preferences for amino acids (and to a lesser extent for carbohydrates) vary substantially among different ant species and may be linked to nectar and honeydew resource partitioning. Preferences are conditional with respect to resource availability and active competition. Therefore, asymmetries in competitive abilities may be crucial and prevent hierarchically inferior ant species from access to more nutritious sources, even when their physiological optima and preferences overlap. Such processes may be fundamental to the territorial mosaic-like distribution of dominant and submissive ants that are common to many tropical ecosystems (Dejean & Corbara 2003).

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Chapter 7 – Trophic analysis using stable isotopes

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Abstract

For diverse communities of omnivorous insects such as ants, the extent of direct consumption of plant-derived resources vs. predation is largely unknown. However, determination of the extent of 'herbivory' among ants may be crucial to understand the hyper-dominance of ants in tropical tree crowns, where prey organisms tend to occur scarcely and unpredictably. We therefore examined nitrogen and carbon stable isotope ratios ($\delta^{15}N$ and $\delta^{13}C$) in 50 ant species and associated insects and plants from a tropical rainforest in North Queensland, Australia. Variation between ant species was pronounced (range of species means: 7.1‰ in $\delta^{15}N$ and 6.8‰ in $\delta^{13}C$). Isotope signatures of the entire ant community overlapped with several herbivorous as well as predacious arthropods. Variability in $\delta^{15}N$ between ants was not correlated with plant $\delta^{15}N$ from which they were collected. Ant species spread out in a continuum between largely herbivorous and purely predacious taxa, with a high degree of omnivory. Ant species $\delta^{15}N$ were consistent with the trophic level predicted by natural feeding observations, but not $\delta^{13}C$. Low $\delta^{15}N$ levels were recorded for nectarivorous ant species on understorey or canopy plants, intermediate levels for species with large colonies that were highly abundant on nectar and honeydew sources and predacious, and the highest levels for predominantly predatory ground-foraging species. Colonies of the dominant weaver-ants (*Oecophylla smaragdina*) had significantly lower $\delta^{15}N$ in mature forests (where preferred honeydew and nectar sources are abundant) than in open secondary vegetation. Nitrogen concentration of ant dry mass showed only very limited variability across species and no correlation with trophic levels. This study demonstrates that stable isotopes provide a powerful tool for quantitative analyses of trophic niche partitioning and plasticity in complex and diverse tropical omnivore communities.

Introduction

The complexity of food webs has challenged theoretical and applied ecology for a long time (see May 1973, Pimm et al. 1991, Post 2002a). Introduction of the concept of trophic levels such as producers, primary consumers, and predators turned out to be useful to structure and analyse food webs. Within trophic levels, the degree of omnivory or specialization continues to be subject to various empirical studies (Reagan & Waide 1996) and was predicted to interact with food web stability (May 1973, McCann et al. 1998). Originally, the position of organisms within food webs was solely based on direct observations as to their mode of nutrient acquisition. However, such observational evidence is difficult and time-consuming to be obtained. Moreover, it often remains critical to decide whether observations over restricted time periods are representative for the nutrient intake of a species in general. The analysis of stable isotope composition of organisms provides an alternative approach. As a consequence of isotopic fractionation associated with many physiological processes, isotope signatures reveal an integrated insight into which nutrient sources a focal organism has used over its lifetime. Stable isotope techniques have entered qualitative analyses of trophic interactions since the work by De Niro and Epstein (1978, 1981), and re-stimulated basic research on underlying processes. This technique has been widely applied to aquatic, marine and shoreline ecosystems (e.g. Cabana and Rasmussen 1994, Post 2002b), larger vertebrates (Hobson 1999, Kelly 2000) and was recently extended to temperate forest soil communities (Ponsard & Arditi 2000, Scheu & Falca 2000) and tropical termites (Boutton et al. 1983, Tayasu et al. 1997, Tayasu 1998). However, studies on other communities remain scarce, particularly from tropical forest systems (but see Hendrix et al. 1999).

Ants perform central functions in most tropical ecosystems, and their biomass often exceeds that of any other animal taxon (Hölldobler & Wilson 1990). Their extraordinary abundance extends well into rainforest canopies where large ant colonies may dominate the entire fauna (Stork 1991, Davidson 1997). Many ants may be largely omnivorous and opportunistic feeders, while some subfamilies and genera comprise highly specialized predators, and others may largely live on vegetarian diets (including seeds, honeydew, plant nectar and food bodies, and fungi) (Stradling 1978, Beattie 1985, Hölldobler & Wilson 1990). The dominance of ants in tropical forest canopies has led to the prediction that canopy ants must gain most of their nutritious requirements as primary consumers (nectar and honeydew) rather than through predation (Tobin 1991, Davidson 1997). Recent observations, supported by modern access methods into the tree crowns, indicated that

most rainforest canopy ant species indeed feed extensively on honeydew and nectar besides prey (Blüthgen et al. 2000b, Dejean et al. 2000), but did not provide quantitative measurements as to how these different resources contribute to the ants' nutrition. It is unknown whether nitrogen-poor plant exudates could be sufficient to sustain the nutritious requirements of ant colonies, or if and how much complementary protein consumption through predation is needed. Isotope studies on ants dwelling in specific myrmecophytic shrubs or epiphytes revealed quite variable proportions of carbon to be obtained directly from plants (Fisher et al. 1990, Rico-Gray & Sternberg 1991, Sagers et al. 2000, Fischer et al. 2002). However, in view of the specialist nature of these ant–plant systems, it is not clear to what extent these results can be generalized to entire communities. On the ant community level, it remains practically unknown how species are partitioned across the isotopic landscape. Preliminary analyses of nitrogen isotope composition from a small number of ant colonies in Panama agree with the hypothesis that dominant canopy ants occupy more basic trophic positions than predators on the ground (Davidson & Patrell-Kim 1996). The goal of the present study was to test this hypothesis in a diverse Australian rainforest ant assemblage in conjunction with detailed observational and experimental studies (*Chapters 2+5*). Our analysis included 50 ant species active in the canopy, understorey and on the ground (but excluding the soil fauna), associated homopterans and plants. Specifically, we addressed the question whether carbon and nitrogen isotope signatures correlate with trophic positions implied by behavioural observations. Trophic effects were tested against alternative hypotheses that variability between ants may be random or caused by plant substrate variability, and these patterns were compared with homopterans. We also examined whether ants (species or colonies) are partitioned between distinct trophic levels (trophic specialization) or continuously distributed between them (omnivory).

Material and Methods

Study site

Samples were collected at two sites in Cape Tribulation (North Queensland, Australia; 16°07' S, 145°27' E). Site-1 is the forest at the Australian Canopy Crane Facility and Site-2 an area within and around the Environmental Research Station, ca. 5 km north of Site-1. Both sites are located in a lowland area (20–80 m a.s.l.) between the coastline and a mountain range and comprise complex mesophyll vine forest (Tracey 1982). Site-1 includes a mosaic of mature forest areas and relatively open natural forest gaps due to severe damage by cyclone 'Rona' in February 1999. Site-2 includes both largely undisturbed mature forest and open

secondary forest < 12 yr of age, dominated by *Macaranga tanarius*. Annual rainfall is ca. 3500 mm, with pronounced seasonality.

Collection methods

Ants and other insects were hand-collected and immediately stored in 70% ethanol, oven-dried at 60°C for 48 h and kept dry until analysis. Prior tests on ants (*Myrmica rubra*) in Germany did not indicate any isotopic effect of alcohol storage. From each adult ant before drying, the gaster was cut off at the petiole and removed from the sample (not applied to ant larvae and pupae or other insects). This method was important to eliminate the effect of undigested food in the ants' crop on isotope measurements. Honeydew-filled gasters from 10 *Oecophylla smaragdina* workers collected while attending homopterans had on average 0.7‰ lower $\delta^{13}C$ and 0.9‰ lower $\delta^{15}N$ values than the remaining body; the C:N ratio was nearly doubled ($n = 2$ comparisons from different colonies, each comprising five workers). Therefore, exclusion of ant gasters was deemed necessary to obtain an unbiased measure of isotopic composition of ant tissues. Samples included 113 colonies from 50 ant species collected from the vegetation (most species) or from the ground. Two dominant ant species, *O. smaragdina* and *Anonychomyrma gilberti*, were represented by 23 vs. 9 different colonies, and further 16 species by 3 colonies each to enable us to recognize intraspecific variability. Each sample contained typically 10 workers from the same colony, but often fewer or more depending on availability and size (between 1 and 30). The coefficient of variation (CV) between three individuals from the same colony was examined for one colony of *O. smaragdina* ($\delta^{13}C$: CV = 1.3%, $\delta^{15}N$: CV = 5.2%) and one of *A. gilberti* (0.7%, 18.4%). $\delta^{13}C$ and $\delta^{15}N$ from pooled samples of 10–15 workers from the same colonies were within ± 0.5 SD units around the mean of these three individuals. Therefore, intracolonial variation of isotope composition was ignored in the present study. We only considered worker ants (usually major workers) collected within or foraging outside their nest, thus disregarding ant sexuals. Larvae and/or pupae were collected from 12 nests of 11 species and major and minor worker castes separately from 8 colonies of 7 species (see Appendix). Ant-tended homopterans included one species each of Aphidae, Membracidae, Cicadellidae and a pooled group of unidentified coccids (total 20 colonies). For comparison and modeling, 11 different arthropods were sampled from plants (Araneae: Thomisidae; Blattodea; Diptera; Heteroptera; Hymenoptera: Apidae; Isopoda; Ensifera: Tettigoniidae; Mantodea; Phasmatodea; Coleoptera: Brentidae; Lepidoptera) and from the ground (Ensifera: Gryllotalpidae).

Plant samples included 13 common species of canopy trees, 5 species of climbing plants, 2 palms and 5 understorey shrubs (total 37 plant individuals). These samples represent plant species commonly visited by ants for extrafloral and floral nectar or honeydew-producing homopterans (*Chapter 2*) and/or characteristic canopy trees that hosted *O. smaragdina* colonies (*Chapter 5*). From all canopy species, sun-exposed leaf samples were collected from the upper tree crown using the crane. Leaf samples were dried in a plant press, ground to fine powder and oven-dried at 60°C. Each sample contained one to several leaf laminae without petioles or twigs. Intraspecific variation was examined for two species, *Entada phaseoloides* and *Syzygium erythrocalyx* (n = 4 vs. 5 individuals), while other plant species were only represented by 1-2 individuals in the analysis.

Isotopic analysis

Samples were weighted on an electronic balance (Sartorius M25D, Göttingen, Germany) and placed in tin capsules (for samples over 40 mg, an aliquot of a homogenate was taken). Isotopic compositions and C and N concentrations of each sample were measured in one run using an elemental analyser – isotope ratio mass spectrometer (EA-IRMS) coupling (EA type 1108, Carlo Erba, Milano, Italy; ConFlo III interface and gas-IRMS delta S, both Finnigan MAT, Bremen, Germany). The deviation of the sample from the international standard in per mil (‰) is expressed as:

$$\delta^{13}C,\ \delta^{15}N\ (‰) = (R_{sample} / R_{standard} - 1) \cdot 10^3,$$

where R_{sample} denotes the ratio between the heavy isotope and its lighter counterpart ($R_{sample} = {}^{13}C/{}^{12}C$, or ${}^{15}N/{}^{14}N$) for the sample, and $R_{standard}$ the ratio for the international standard (N_2 in the air and CO_2 in PeeDee belemnite), respectively. N_2 or CO_2, respectively, from lecture bottles calibrated against the reference substances N1 and N2 for the N isotopes or NBS 19 and ANU sucrose for the C isotopes was used as laboratory standard (Gebauer & Schulze 1991). All reference substances were provided by the International Atomic Energy Agency, Vienna. Reproducibility of the isotope measurements for N_2 or CO_2, respectively, based on the above-described equipment is typically ± 0.15‰ or better. Reproducibility was routinely controlled by measurement of acetanilide (MERCK, Germany). Acetanilide was furthermore used to calibrate C and N concentration measurements (Gebauer & Schulze 1991).

Data analysis

In order to compare isotope data with observations on ant feeding behaviour, we used published information about ant genera (Briese & Macauley 1981, Andersen 1995, Shattuck 1999 and references therein) and our own observations of ant species from the study site. Nectar and honeydew feeding was observed between 1999 and 2002 (data in *Chapter 2*). Sugar feeding was also tested using artificial sugar solutions in plastic tubes tied to tree trunks throughout the forest for several months in 2001 and 2002 (*Chapter 6*). Natural fruit feeding was examined once in February 2000 for 50 fruits with fleshy yellow arils from a *Synima cordierorum* (Sapindaceae) tree, each placed on a paper sheet on the ground along a ca. 500 m transect through the forest and repeatedly surveyed over 6 h.

The question whether isotopic signatures vary between ant species and subfamilies was addressed using multiple analysis of variance (MANOVA) for both variables $\delta^{13}C$ and $\delta^{15}N$. In case of significance, univariate tests of $\delta^{13}C$ and $\delta^{15}N$ were performed. Isotope data did not deviate significantly from normal distribution (Kolmogorov-Smirnov tests, $p > 0.05$). In order to examine the effect of variation between plants, we compared isotope values from ant and homopteran samples with the foliage of the plant from which they were collected (total 60 plant-ant pairs, including 32 samples from the same plant individual and 28 from a different individual of the same plant species; 22 plant-homopteran pairs: 20 from the same plant individual, 2 from the same species).

Omnivory was tested against the null hypothesis that the variance (σ^2) of $\delta^{13}C$ or $\delta^{15}N$ between ant species is not significantly larger than expected (Ponsard & Arditi 2000). Expected values are variances in trophic enrichment (Δ) of animals compared to their diet: $\sigma^2_\Delta(\delta^{13}C) = 1.96‰$, $n = 76$ and $\sigma^2_\Delta(\delta^{15}N) = 1.21‰$, $n = 26$ (Gearing et al. 1984, Mingawa & Wada 1984, Ponsard & Arditi 2000). The test is considered conservative

since variability within a single taxon (ants) is probably smaller than between various vertebrates and invertebrates considered by the above studies.

Results

Plants

Leaf samples (species listed in the Appendix) showed some variation in isotope signatures (Figure 1a; mean ± SD, range: $\delta^{13}C$ = -28.6 ± 1.8‰, -25.2 to -31.6‰; $\delta^{15}N$ = 2.1 ± 1.5‰, -0.4 to 5.0‰, n = 37 samples). No evidence was found for obligate crassulacean acid metabolism (CAM) or C_4 photosynthesis among the 25 species (typical $\delta^{13}C$ > -20‰, see Winter et al. 1983). One legume liana species (*Entada phaseoloides*) had a mean $\delta^{15}N$ similar to atmospheric N_2 ($\delta^{15}N$ = 0.4 ± 0.8‰, n = 4), generally indicative of N_2-fixation; some myrtaceous and lauraceous trees had relatively low values as well. However, the overall low ^{15}N abundance in this study site and the limited sample size makes distinctions between nodulating and non-nodulating plants highly problematic (Shearer & Kohl 1988, Guehl et al. 1998). Högberg (1997) recommended that only differences in $\delta^{15}N$ of more than 5‰ are meaningful to distinguish N_2-fixing from non-nodulating plants, thus the variation in our study site is well below this threshold. Variability between conspecific plants was very high (see Figure 1a), particularly for $\delta^{15}N$ in *Syzygium erythrocalyx* (ranging from 0.2 to 4.2, n = 5). Across species samples from the two sites did not differ in $\delta^{13}C$ and $\delta^{15}N$ (MANOVA: Rao's $R_{2, 35}$ = 0.79, p = 0.46), and no difference was found between samples from mature forests from both sites vs. young secondary forest from Site-2 ($R_{2, 35}$ = 0.42, p = 0.66). Therefore, data from both sites were pooled for the following analyses.

Homopterans

Isotope signatures of homopterans (listed in Appendix) showed a similar range as plants. In general, isotope concentrations of homopterans correlated significantly with those of their host plant foliage ($\delta^{15}N$: Pearson's r = 0.79, p < 0.001; $\delta^{13}C$: r = 0.56, p = 0.01, n = 20 pairs) (dotted lines in Figure 1a). However, in membracids and cicadellids (both Auchenorrhyncha), all samples except one were more enriched in ^{13}C than their host plant foliage (mean difference to host plant ± SD: 1.7 ± 1.1‰, range: -0.3 to 2.7‰, n = 9). The ^{15}N concentration of cicadellids was consistently above the plant level (mean difference 0.2 to 1.6‰, n = 3), but more variable in membracids where four of six samples were ^{15}N

depleted (-1.3 to 0.9‰, n = 6). Inversely, Sternorrhyncha (coccoids from four families and aphids) were invariably enriched in ^{15}N compared to their hosts (1.4 ± 0.6‰, 0.4 to 2.2‰, n = 9), but more variable and mostly depleted in ^{13}C (-1.1 ± 1.8‰, -4.1 to 1.9‰).

Ants

Isotope signatures of ants (listed in Appendix) covered a broad range, encompassing 7.1‰ in $\delta^{15}N$ and 6.8‰ in $\delta^{13}C$, thus exceeding two typical transfers between trophic levels in nitrogen (3.4‰) (Figure 1b). The range of ants overlaps with several arthropod orders that include typical predators or herbivores (Figure 1a). No significant correlation was found between $\delta^{15}N$ of ants and $\delta^{15}N$ of plant individuals or species from which they were collected (Pearson's r = 0.22, p = 0.09, n = 59 sample pairs), while $\delta^{13}C$ signatures showed a weak positive correlation (r = 0.35, p < 0.01). $\delta^{15}N$ was consistently low in all *Camponotus* and most *Polyrhachis* species as well as several other ants that were frequently observed at extrafloral and floral nectaries (e.g. *Echinopla australis, Tapinoma minutum, Tetraponera nitida*) (for foraging observations, see Appendix). $\delta^{15}N$ levels were increased in *Anonychomyrma gilberti*, and much more so in *Oecophylla smaragdina*. Both species had very large colonies and were highly dominant on honeydew and nectar sources particularly in the canopy of the study site, but also regularly observed preying on various arthropods. Some subdominant ant species with large colonies were common on nectar and honeydew sources in the understorey (*Crematogaster* cf. *fusca, Paratrechina vaga, Rhoptromyrmex wroughtonii*, *Technomyrmex albipes*), but more enriched in ^{15}N than the previous species. Exclusively ground-foraging ant species showed the highest $\delta^{15}N$ levels. These included army ants (*Aenictus atratus*) and *Leptogenys* species which are known as being solely predacious (Shattuck 1999). Other ponerine ants (genera *Heteroponera, Rhytidoponera, Odontomachus*) may be typically predators or scavengers (Briese & Macauley 1981, Shattuck 1999) although they were repeatedly observed feeding from extrafloral nectaries or artificial sugar solutions. Some *Pheidole* species and *Pheidologeton affinis* were predominantly ground-foraging, but besides predation and scavenging, occasional seed or fruit flesh consumption (Appendix; Briese & Macauley 1981) may play a certain role.

On the community level omnivory of ants was confirmed by nitrogen but not carbon isotopes in a null model test proposed by Ponsard and Arditi (2000): the variance of $\delta^{15}N$ among all ant species (σ_a^2 = 4.4‰) was significantly larger than the expected variance of

trophic transfers ($F_{49, 25} = \sigma_a^2 / \sigma^2_\Delta = 3.6$, $p < 0.001$), but not for $\delta^{13}C$ ($\sigma_a^2 = 1.5‰$, $F_{49, 75} = 0.8$, $p = 0.87$).

$\delta^{13}C$ and $\delta^{15}N$ in ant species were significantly correlated ($r = 0.31$, $p < 0.05$). Isotopic signatures varied significantly between ant species and subfamilies. Both $\delta^{15}N$ and $\delta^{13}C$ contributed significantly to the variation between species (ANOVA: $\delta^{15}N$: $F_{17, 62} = 10.2$, $p < 0.001$; $\delta^{13}C$: $F_{17, 62} = 15.9$, $p < 0.001$). Interspecific variability was also significant when isotope values for plants from which each ant colony had been collected were included as covariate (ANCOVA: $\delta^{15}N$: $F_{15, 34} = 8.6$, $p < 0.001$; $\delta^{13}C$: $F_{15, 34} = 11.4$, $p < 0.001$). The four major ant subfamilies differed significantly only in $\delta^{15}N$ ($F_{3, 44} = 17.7$, $p < 0.001$), but not in $\delta^{13}C$ ($F_{3, 44} = 0.8$, $p = 0.51$). Isotope signatures of 23 *Oecophylla smaragdina* colonies are displayed in Figure 2. No significant variation was found between the two sites (MANOVA: $F_{2, 20} = 1.6$, $p = 0.23$), but there was a pronounced effect of successionary forest stages: colonies in recently reforested areas at Site-2 had significantly lower $\delta^{15}N$ than those from mature complex forests both at Site-1 and Site-2 (ANOVA: $F_{1,21} = 24.7$, $p < 0.001$). This effect was not found for $\delta^{13}C$ ($F_{1,21} = 0.2$, $p = 0.69$).

Ant larvae differed from adults in isotopic composition (species marked in Appendix). In six out of seven species tested, $\delta^{13}C$ increased from larvae to adult workers (by 0.03–2.5‰, except for a 0.8‰ decrease in a *T. albipes* colony) as well as $\delta^{15}N$ (by 0.01–1.4‰ except for a 1.1‰ decrease in *A. gilberti*). Isotope composition also increased from pupae to adults in five out of six species (by 0.9–2.0‰ in $\delta^{13}C$ and 0.1–0.6‰ in $\delta^{15}N$, except for *E. australis*). The overall trend from larvae (or pupae where no larvae had been sampled) to adults across all 11 species was significant for $\delta^{13}C$, but not for $\delta^{15}N$ (Wilcoxon matched pairs: $\delta^{13}C$: $Z = 2.2$, $p < 0.05$; $\delta^{15}N$: $Z = 1.2$, $p = 0.24$, $n = 12$ colonies). Differences in isotope composition were also found between worker castes. There was a consistent trend in $\delta^{15}N$ across six colonies from five species where samples included head and alitrunk (marked in Appendix): major workers had a significantly lower $\delta^{15}N$ than minors (reduced by 0.3–1.1‰, $Z = 2.2$, $p < 0.05$), while $\delta^{13}C$ did not vary significantly between castes ($Z = 0.9$, $p = 0.35$). This trend for $\delta^{15}N$ was not found in pupae that would have developed into major and minor workers (differences in $\delta^{15}N < 0.1‰$, $n = 2$ species), indicating that differential isotope signatures of castes may result from processes during metamorphosis or adult life stages. Furthermore, when only the heads of major and minor workers were analysed, caste differences were negligible (differences in $\delta^{15}N < 0.2‰$, $n = 2$).

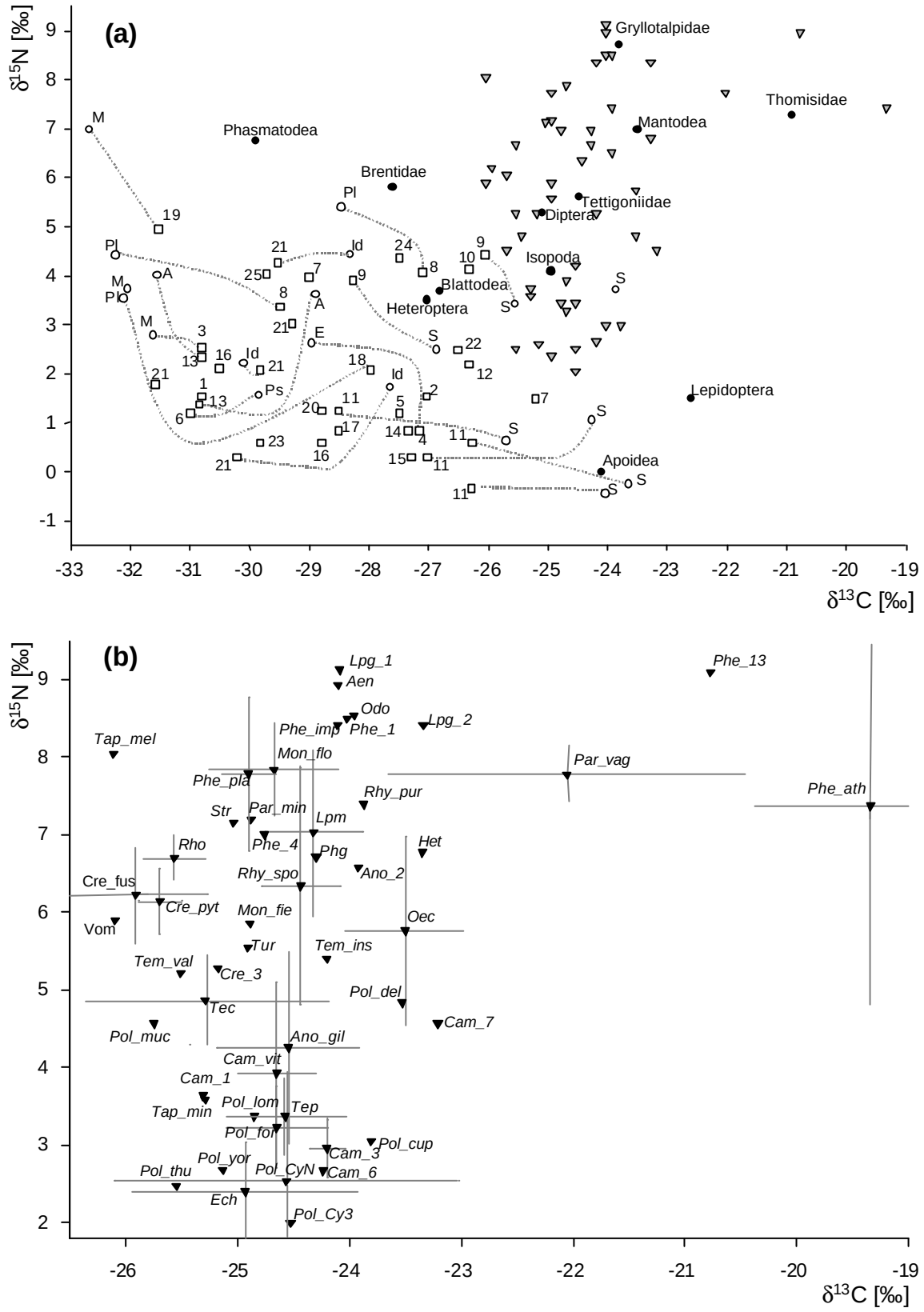

Fig. 1 Isotope composition ($\delta^{13}C$ and $\delta^{15}N$) of (a) plants, homopterans and other arthropods and (b) ants from the study site. Plants are represented by squares (with number code), homopterans by open circles (with letter code), other arthropods by black circles, and ants by triangles (both a and b). Homopterans and their respective host plant individual are connected by a dotted line. Each ant species with multiple sampled colonies is represented by its mean and standard deviation bars (for sample size and full species names, see Appendix).

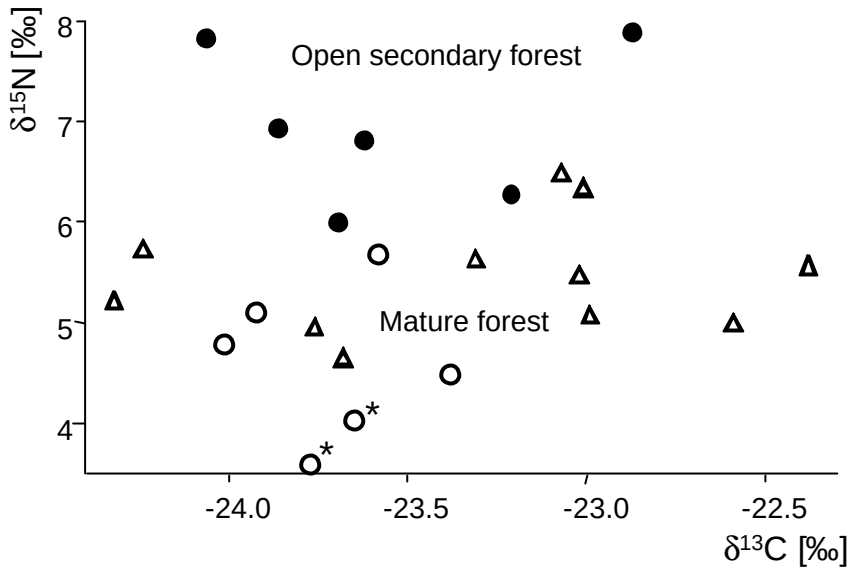

Fig. 2. Isotope signatures of 23 *Oecophylla smaragdina* colonies. Site-1 is represented by triangles, Site-2 by closed circles (naturally regenerating forest) or open circles (mature forest). Two colonies from a mature beach forest near Site-2 are marked with an asterisk.

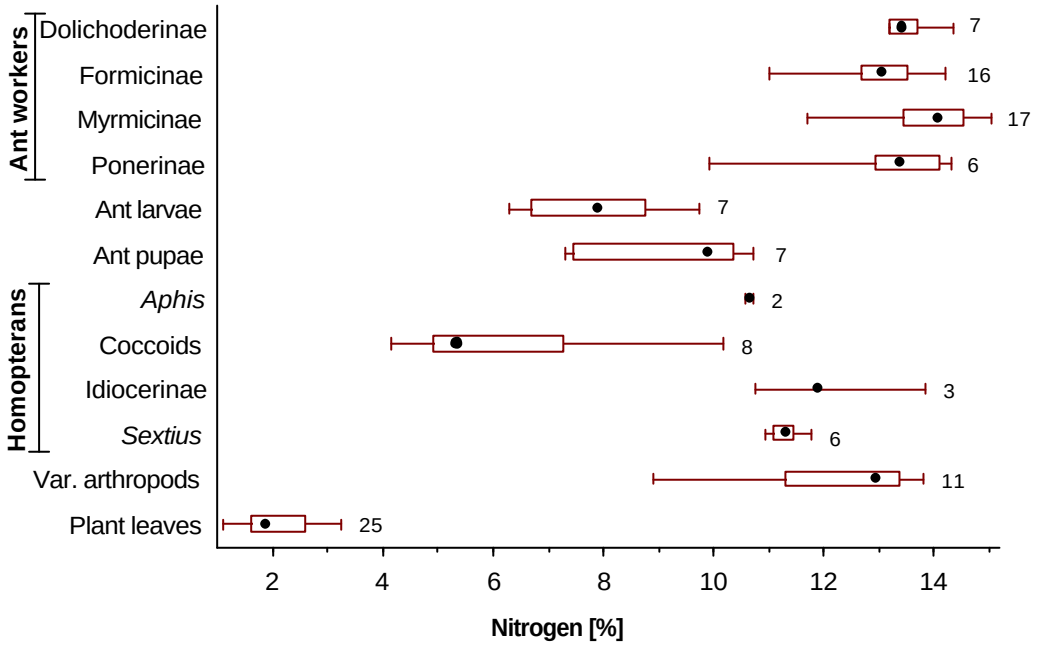

Fig. 3. Nitrogen concentration (per cent dry weight) in adult workers from four ant subfamilies, ant brood, homopteran taxa, various arthropods and plant leaf material. Numbers are sample sizes (numbers of species in ant workers and plants, otherwise number of samples).

C and N concentrations

Dry mass carbon and nitrogen concentrations (M_C and M_N, respectively) showed relatively little variation across workers of different ant species (mean ± SD; M_C: 51.4 ± 3.3%, M_N: 13.4 ± 1.0%, C:N ratio: 3.8 ± 0.4). No significant correlation was found between M_N and $\delta^{15}N$ (r = 0.10, p = 0.50) or between C:N ratio and $\delta^{15}N$ (r = -0.07, p = 0.65). The same conclusions hold true when ant genera instead of species are used as units (M_N and $\delta^{15}N$:

$r = 0.18$, $p = 0.40$; C:N and $\delta^{15}N$: $r = -0.15$, $p = 0.48$). Furthermore, M_N showed only little and marginally significant variation between the four major ant subfamilies (Figure 3; $F_{3, 42} = 2.5$, $p = 0.07$). No significant difference in M_N was found between ant species that attended homopterans and the rest of the ant community ($F_{1, 46} = 1.0$, $p = 0.32$). M_N was significantly lower for ant larvae and pupae (Figure 3) than for adult workers of the same colony (paired t-tests; adults vs. larvae: $t = 11.9$; adults vs. pupae: $t = 9.6$, $p < 0.001$). The four homopteran taxa had significantly lower M_N than ant workers (Figure 3; $F_{1, 50} = 31.8$, $p < 0.001$) and significantly higher C:N ratios (6.2 ± 3.2%; $F_{1, 49} = 28.3$, $p < 0.001$).

Discussion

Nitrogen isotope signatures of 50 Australian rainforest ant species are consistent with the hypothesis that ant communities represent a continuum from herbivores to predators, with pronounced omnivory. Species or genera that are regarded as predominantly predators and scavengers (see Briese & Macauley 1981, Shattuck 1999) had consistently high ^{15}N concentration, while ant species regularly feeding on nectar or honeydew (*Chapters 2+5*) were relatively ^{15}N depleted. Other studies also concluded that $\delta^{15}N$ but not $\delta^{13}C$ correlate with predicted trophic positions in a soil food web (Ponsard & Arditi 2000). Several lines of evidence suggest that variation of $\delta^{15}N$ among ants depict real trophic positions rather than sheer plant substrate variability from which ants were collected. (1) There was no correlation between $\delta^{15}N$ of ants and plants, while plant-sucking homopterans and their hosts were strongly correlated. In contrast, $\delta^{13}C$ data of both ants and homopterans varied significantly with plant signatures and may be a better indicator of substrate (of nectar, honeydew or prey) rather than trophic position. (2) Interspecific variability between ants was independent of covariance with plant substrate. (3) Focusing the food web analysis on a narrowly defined, but species-rich taxonomic group – ants – has the advantage to limit effects of different biochemical pathways and body types that could confound differences in diets, since little is known about net fractionation from many invertebrates and several other processes that may further complicate conclusions about trophic interactions (see Gannes et al. 1997). (4) From observations of their natural foraging behaviour, it can be inferred that most ant colonies derive their food sources from various plant species (personal observation). Extreme host plant specificity is the rule among ants on true myrmecophytes (Sagers et al. 2000, Fischer et al. 2002), but such close associations did not occur at the study site.

Results from our isotope analyses (see also Davidson & Patrell-Kim 1996) support Tobin's (1991) hypothesis that honeydew and nectar are important diets of many canopy ants. Tobin suggested that the numerical abundance of ants in rainforest canopies could only be sustained if they were primary consumers rather than predators, because prey availability would be too limited ('biomass paradox'). However, the simplification that these ants must be 'chiefly' herbivores has to be considered with caution, and our results demonstrate a far more complex picture and pronounced asymmetry in source partitioning. Many canopy ant species, typically those that are inferior in the dominance hierarchy and have small to intermediate colonies (Hölldobler 1983, Andersen 1995, own observations), occupied very basic positions in the food web (*Camponotus*, *Echinopla*, *Polyrhachis*, *Tetraponera*). Since these species were not observed to attend homopterans in the study site (although these four genera are generally known as trophobiotic elsewhere), their main diets should be extrafloral and floral nectar or other plant-based sources. In contrast, the dominant canopy ants (*Oecophylla*, *Anonychomyrma*) have intermediate and the subdominant understorey ants (*Crematogaster*, *Paratrechina*, *Rhoptromyrmex*, *Technomyrmex*) higher trophic positions. These ants regularly attend homopterans, they are among the most abundant nectar foraging species at the study site, and their distribution is strongly influenced by productive honeydew sources that are more predictable than prey (*Chapters 2+5*). However, their large colonies also seem to gain substantial parts of their nutrition through predation. Due to their high activity, competitive ability and aggressiveness, the dominant ants may even be more effective predators than submissive ants (e.g. Way 1953). Prey is an important component of the omnivorous diet in *Oecophylla* (see also Floren et al. 2002). Intraguild predation may be pronounced, since ant corpses provide large proportions of prey caught by *Oecophylla* (personal observation) or other ants (Briese & Macauley 1981). The complex ant community, including feedback loops through intraguild predation, may thus represent an important proportion of the entire food web in the forest. The highest levels of predation as judged by $\delta^{15}N$ signatures are found for ants that are most active in the understorey or completely ground-foraging.

Dietary plasticity between colonies of the same ant species can be pronounced. *Oecophylla* colonies in young secondary forests were more enriched in ^{15}N compared to adjacent mature forest, although plants collected from both sites had similar isotope composition. In the complex canopy of mature forests, these ants often attend large homopteran aggregations, particularly on two legume lianas (*Chapter 5*). These homopteran hosts were absent from recently reforested sites, and trophobioses seemed to be generally less

established. Many preferred nectar plants were also more common in, or completely confined to, complex forests. Several pioneer euphorb shrubs with extrafloral nectaries were abundant in secondary habitats, but their nectar usually attracted other ant species and was rarely attended by *Oecophylla* (*Chapter 2*). Thus, suitable honeydew and nectar sources in mature forests allow *Oecophylla* to include them as significant part of their nutrition, while colonies in secondary habitats may be more predacious. The trophic plasticity of *Oecophylla* may potentially affect their effectiveness in biological pest control of agroecosystems for which this species is commonly used (Way 1953, Peng et al. 1999).

The stable isotope composition of ant workers should largely reflect their larval diet except for possible effects of ageing, because these holometabolous insects do not gain any additional somatic biomass as adults, and oogenesis is quantitatively unimportant if not absent in the worker caste. It is commonly assumed that proteins are preferentially fed to larvae in ants while sugars are mainly used for worker metabolism (Vinson 1968, Haack et al. 1995), so adult foraging for nectar and honeydew may show an even higher proportion of plant diet than calculated from isotope composition. This may explain the apparent discrepancies between observations and isotope results in those ant species that commonly attended homopterans in the understorey (*Crematogaster, Paratrechina, Rhoptromyrmex, Technomyrmex*) and were among the most frequent ants on nectaries as well. Isotope signatures of larvae and pupae from 10 species were indeed very similar to adults in our study. Only a slight increase in $\delta^{15}N$ (and sometimes $\delta^{13}C$) was found that might be explained by the direct contribution of the stomach content in larvae (empty in pupae and removed from adults), or by ageing (see Ponsard & Averbuch 1999 for general effects of ontogeny). The same trend during ontogeny was found elsewhere for ant species feeding on plant food bodies (Sagers et al. 2000, Fischer et al. 2002). The small but consistent difference between major and minor workers (also reported by Fischer et al. 2002, but variable in termites: Tayasu et al. 1997) may be similarly caused by multiple factors (Tayasu 1998).

Davidson and Patrell-Kim (1996) proposed that canopy ants which live on nitrogen-poor plant exudates may have developed mechanisms to reduce nitrogen requirements, e.g. through a thinner exoskeleton. They suggested that herbivorous ants might have reduced nitrogen concentrations and found some support to this idea in a preliminary analysis of 11 ant species in Panama. However, in our study carbon and nitrogen dry weight concentrations were remarkably constant across the ant community, and no correlation with trophic position was found. Morphological and physiological constraints may strongly

limit the capability to save nitrogen to a great extent. 'Classical' herbivores such as homopterans showed much lower nitrogen concentrations. Other strategies proposed by Davidson (1997) include nitrogen-poor chemical defence or 'high tempo' activity, and may be more powerful to explain the ants' success in the canopy habitats.

Nectar and honeydew are often seen as mainly carbohydrate sources, because of their high C:N ratio compared to meat. Several studies have thus focused on carbon isotope composition of ants (Fisher et al. 1990, Rico-Gray & Sternberg 1991, Sagers et al. 2000). However, our results about nitrogen isotopes emphasize the important contribution of nitrogen from these plant-based resources (see also Fischer et al. 2002). Further studies using controlled diets will be needed to evaluate the proportions of carbon and nitrogen flows from different sources and compounds, and differential effects of isotopic fractionation. Curiously, $\delta^{15}N$ of ants showed a greater overlap with plant foliage than $\delta^{13}C$. Limited evidence from few studies suggests that different plant products and tissues vary in isotope composition (Gleixner et al. 1993, Bauer et al. 2000, Schmidt & Stewart 2003), and such differences may be linked to the observed pattern. For example, plant leaf tissues may not equally represent $\delta^{15}N$ and $\delta^{13}C$ of nectar or honeydew consumed by ants.

Plant samples from our study site showed low overall ^{15}N abundance and no indication of CAM- or C_4-metabolism. The observed level and variability of plant $\delta^{13}C$ in Australia is typical for C_3-plants in other rainforests (Guehl et al. 1998, Bonal et al. 2000, Nagy & Proctor 2000), while C_4 or CAM may be more prominent in other habitats and life forms, such as epiphytes. However, none of the Australian epiphytic genera known to utilize CAM (Winter et al. 1983) were common at the study site.

Although there was a significant overall correlation between isotope signatures of homopterans and their individual host plants, pairwise differences revealed a characteristic pattern. While aphids and coccoids (both Sternorrhyncha) were often ^{15}N-enriched and ^{13}C-impoverished compared to plant foliage (also found for aphids by Ostrom et al. 1997), membracids and cicadellids (both Auchenorrhyncha: Cicadelloidea) were ^{13}C-enriched and variable in ^{15}N. Sternorrhyncha are assumed to feed predominantly on phloem sap, while Cicadelloidea ingest sap from xylem, phloem, and parenchyma (Carver et al. 1994). Assuming isotopic differences between plant tissues and compounds as mentioned above (Gleixner et al. 1993, Bauer et al. 2000, Schmidt & Stewart 2003), variation between homopterans and leaf samples may thus be linked to these variable feeding modes of homopterans. Besides substrate effects, the digestive microfauna of homopterans may also influence their stable isotope composition. Relations between isotope signatures of termites

and their substrate were highly variable (Tayasu et al. 1997), and this variation was attributed to diverse associations with intestinal microorganisms. Further studies are needed to evaluate if different isotope signatures can be used to detect differences in substrate use and microfaunal activity between homopteran taxa.

In conclusion, stable isotope techniques proved to be a useful tool for studies of resource partitioning in a complex tropical community of omnivorous insects where other methods to quantify trophic positions are largely ineffective. Nitrogen isotopes indicate a pronounced inter- and intraspecific plasticity in resource use among ants. Herbivory may be most developed in ants with small to intermediate colonies that forage on understorey or canopy plants, while predation is most pronounced in ground-foraging species. *O. smaragdina* and all subdominant understorey ant species showed intermediate trophic levels indicating a significant contribution of predation as well as trophobioses and nectarivory. Particularly in canopy ants, honeydew and nectar may not only supply carbon for adult metabolism, but also serve as an important source of nitrogen for larval growth.

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Appendix. Ant, plant and homopteran species and their codes used in Figure 1. Sample sizes (*n*) are number of ant or homopteran colonies or plant individuals analysed. Observation of ant foraging on plant foliage, nectar feeding, honeydew feeding, feeding on fruit flesh or sugar solutions indicated by P, N, H, F, and S respectively. G marks species that were only observed on the ground or lower tree trunks.

Code	(Sub-)family	Species	Foraging observ.	*n*
Ants (Hymenoptera: Formicidae)				
Aen	Aenictinae	*Aenictus aratus* Forel	G	1
Ano_gil	Dolichoderinae	*Anonychomyrma gilberti* (Forel)	PNHS	9
Ano_2		*A.* sp2	PN	1
Lpm		*Leptomyrmex unicolor* Emery	PNFS	3
Tap_mel		*Tapinoma melanocephalum* (Fabricius) [1])	PNS	1
Tap_min		*T. minutum* Mayr	PNS	1
Tec		*Technomyrmex albipes* (Smith) [1]) [2])	PNHS	3
Tur		*Turneria bidentata* Forel [1])	PN	1
Cam_1	Formicinae	*Camponotus* sp1 (*macrocephalus* gp.)	PNS	1
Cam_3		*C.* sp3 (*novae-hollandiae* gp.) [4])	PNS	3
Cam_6		*C.* sp6 (*gasseri* gp.)	PNS	1
Cam_7		*C.* sp7 (*extensus* gp.) [3])	PS	1
Cam_vit		*C. vitreus* (Smith) [1]) [2]) [3]) [5])	PNS	3
Ech		*Echinopla australis* Forel [2]) [2])	PNS	3
Oec		*Oecophylla smaragdina* (Fabricius) [1]) [2]) [3]) [3]) [5])	PNHS	23
Par_min		*Paratrechina minutula* (Forel)	PNS	1
Par_vag		*P. vaga* (Forel) [1])	PNHFS	3
Pol_Cy3		*Polyrhachis* (*Cyrtomyrma*) 'Cyrto 03' Kohout	PN	1
Pol_CyN		*P.* (*Cyrtomyrma*) 'Cyrto NB5041' Kohout [4])	PNS	3
Pol_yor		*P.* (*Cyrtomyrma*) *yorkana* Forel	PNFS	2
Pol_thu		*P.* (*Hagiomyrma*) *thusnelda* Forel	PN	1
Pol_cup		*P.* (*Hedomyrma*) *cupreata* Emery	PNS	1
Pol_for		*P.* (*Myrma*) *foreli* Kohout	PNS	3
Pol_lom		*P.* (*Myrmatopa*) *lombokensis* Emery	P	1
Pol_muc		*P.* (*Myrmhopla*) *mucronata* Smith	PNS	1
Pol_del		*P.* (*Myrmothrinax*) *delicata* Crawley	PNS	1
Cre_fus	Myrmicinae	*Crematogaster* cf. *fusca* Smith	PNHS	3
Cre_pyt		*C.* cf. *pythia* Forel [2])	PNS	3
Cre_3		*C.* sp3	PNS	1
Mon_fie		*Monomorium fieldi* var. *laeve-nigrius* Forel	PNS	1
Mon_flo		*M. floricola* Forel [2])	PNS	3
Phe_imp		*Pheidole impressiceps* Mayr	PNFS	1
Phe_pla		*P. platypus* Crawley [3])	PNFS	3
Phe_1		*P.* sp1	PNFS	1
Phe_4		*P.* sp4	GF	1
Phe_13		*P.* sp13	PH	1
Phe_ath		*P.* cf. *athertonensis* Forel [2]) [3])	PNFS	3
Phg		*Pheidologeton affinis* (Jerdon)	GFS	1
Rho		*Rhoptromyrmex wroughtonii* Forel	PNHS	3
Str		*Strumigenys guttulata* Forel	PN	1
Tem_ins		*Tetramorium insolens* (F. Smith)	PNS	1
Tem_val		*T. validiusculum* Emery	PNS	1
Vom		*Vombisidris australis* (Wheeler)	P	1
Het	Ponerinae	*Heteroponera* sp1	PS	1
Lpg_1		*Leptogenys* sp1	G	1
Lpg_2		*L.* sp2	G	1
Odo		*Odontomachus ruficeps* Smith	PNFS	1
Rhy_pur		*Rhytidoponera purpurea* (Emery)	PS	1
Rhy_spo		*R. spoliata* (Emery)	PNS	3
Tep	Pseudomyrmecinae	*Tetraponera nitida* (Smith)	PNS	3

Additional sampling of [1]) larvae, [2]) pupae or [3])-[5]) minor and major caste separately: [3]) worker head and alitrunk, [4]) worker head only and [5]) pupae.

Appendix (continued).

Code	(Sub-)family	Species	*n*
'Homoptera' (Hemiptera: Sternorrhyncha and Auchenorrhyncha)			
A	Aphidae	*Aphis clerodendri* Matsumura	2
Id	Cicadellidae	Idiocerinae: Gen. nov.	3
M	Coccidae	*Milviscutulus mangiferae* (Green)	3
Ps	Diaspididae	*Pseudaulacaspis* sp.	1
E	Eriococcidae	(Genus not identified)	1
S	Membracidae	*Sextius 'kurandae'*	7
Pl	Pseudococcidae	*Planococcus minor* (Maskell)	3
Plants			
1	Arecaceae	*Licuala ramsayi* (F.Muell) Domin	1
2		*Normanbya normanbyi* (W.Hill) L.H.Bailey	1
3	Asclepiadaceae	*Melodinus australis* Pierre	1
4	Convolvulaceae	*Merremia peltata* Merr.	1
5	Eleocarpaceae	*Elaeocarpus angustifolius* Blume	1
6	Euphorbiaceae	*Aleurites rockinghamensis* (Baill.) P.I.Forster	1
7		*Macaranga involucrata mallotoides* (F.Muell.) L.M.Perry	2
8		*M. tanarius* Muell. Arg.	2
9	Fabaceae *s.l.*	*Caesalpinia traceyi* L. Pedley	2
10		*Castanospermum australe* A.Cunn.& C.Fraser ex Hook.	1
11		*Entada phaseoloides* Merr.	4
12	Flagellariaceae	*Flagellaria indica L.*	1
13	Lamiaceae	*Clerodendrum tracyanum* (F.Muell.) Benth.	1
14	Lauraceae	*Cryptocarya hypospodia* F.Muell.	1
15		*C. murrayi* F.Muell.	1
16		*Endiandra microneura* C.T. White	2
17	Meliaceae	*Dysoxylum pettigrewianum* F.M.Bailey	1
18	Moraceae	*Ficus destruens* C.T. White	1
19	Myrsinaceae	*Ardisia pachyrrhachis* (F.Muell.) F.M.Bailey	1
20	Myrtaceae	*Acmena graveolens* L.S. Smith	1
21		*Syzygium erythrocalyx* B.Hyland	5
22		*S. gustavioides* (F.M.Bailey) B.Hyland	1
23		*S. sayeri* (F.Muell.) B.Hyland	1
24	Proteaceae	*Cardwellia sublimis* F.Muell.	1
25	Sterculiaceae	*Argyrodendron peralatum* (Bailey) Edlin ex J.H.Boas	1

Synopsis

Overview The seven main chapters of this thesis encompass analyses of community *patterns* and underlying *processes*. First, nectar and honeydew sources from an Australian rainforest and observations of their use by ant communities were described. Secondly, analyses of their sugar and amino acid composition and experiments on the ants' preferences for these compounds were used to approach causal mechanisms that shape the ant community.

Patterns – Ant communities and their plant-based diets

Diversity and distribution of nectar and honeydew sources

Extrafloral nectaries Thirty-four plant species from 30 genera and 16 families were found to provide extrafloral nectaries (EFNs) in the Australian rainforest studied (*sensu* Zimmermann 1932, including circumfloral nectaries) **(Chapter 1)**. These cases include 12 genera from which EFNs have not been recorded in the literature to date (see Elias 1983, Koptur 1992). In the study site, EFN-bearing plants represented 13 tree species (16.9% of the trees identified in a one-hectare plot), 12 climbing plant species (21.3% of those examined for EFN presence) and eight species of shrubs. A significantly higher abundance of EFN-bearing shrubs was found in open forest gaps than in closed forest patches. The proportion of EFN-plants in the local flora and their abundance in the vegetation is comparable with studies from other tropical forest outside Australia. However, most genera with EFNs in this study are characteristic Indomalayan elements, while only two genera and 12 species are endemic to Australia including adjacent Pacific Islands. Morphological structures of investigated EFN represented five structural types defined by Zimmermann (1932) and Elias (1983): flattened, elevated, pit, scale-like, and formless nectaries.

Floral nectar sources EFNs from all plant species were visited by ants. Besides EFNs, ants were found to consume floral nectar from 17 plant species **(Chapter 2)**. While ants were the most common visitors of EFNs compared to any other arthropod taxon (typical for most EFNs, see Koptur 1992), they were generally less abundant on flowers. For some plant species, ants were never observed to

consume floral nectar although they were foraging in the vicinity of flowers. Examples include narrow flower tubes that were not accessible to most ant species, but also floral nectars from open accessible flowers. When such accessible nectars were presented in plastic tubes **(Chapter 3)**, they were either significantly less attractive to ants than a sugar solution with the same concentration (*Syzygium gustavioides*, sterile stigma nectar of *Normanbya normanbyi*), or attracted ants in the same way as the sugar control (*Acmena graveolens*). The first two cases suggest that these nectars include repellents against ants. Ant-repellent floral nectars have been implied by Janzen (1977) whose paper provoked a contentious debate (Guerrant & Fiedler 1981, Haber et al. 1981, Beattie et al. 1984, Koptur & Truong 1998, Adler 2000, Ghazoul 2001).

Wound sap Wound sap exudates represent another resource that was regularly exploited by ants **(Chapters 2+3)**. These sources include scars from flower abscission on palms (*N. normanbyi*) and bitemarks on the foliage of trees (*Cardwellia sublimis, Syzygium sayeri*). Wound sap use by ants has been poorly documented in the literature thus far (Tobin 1994).

Honeydew producers A broad spectrum of honeydew-producing homopterans was attended by ants **(Chapter 2)**. These trophobiotic interactions (general overviews provided by Way 1963, Buckley 1987, Hölldobler & Wilson 1990) included 12 species from the suborders Auchenorrhyncha (cicadellids, membracids) and Sternorrhyncha (aphids, coccids, eriococcids, diaspidids, margarodids, pseudococcids). Other trophobionts were two species of lycaenid caterpillars attended by *Oecophylla smaragdina* **(Chapter 5)**. Trophobiotic interactions on common *Clerodendrum tracyanum* shrubs involving aphids (*Aphis clerodendri*) were of particular biogeographical interest, since few aphid species are assumed to be native to Australia. *A. clerodendri* is specialised on plants of the genus *Clerodendrum* where they induce galls on stems or leaves **(Chapter 4)**. However, most other trophobionts in this study were broadly polyphagous. Trophobiotic activity of *O. smaragdina* was monitored over two years. The total abundance of honeydew producing homopterans and attending ant workers was found to be maintained at a high level throughout wet and dry months, particularly on lianas **(Chapter 5)**. In contrast, secretory activity of many EFNs was largely reduced during drier periods **(Chapter 1)**, and

production of floral nectar was *per se* temporally restricted to individual flowering periods.

Ant communities at nectar and honeydew sources

Ant species richness

Overall, 43 ant species were observed to consume nectar from flowers or EFNs **(Chapter 2)**. Randomised ant species accumulation curves (based on plant individuals from which they were collected) indicate that these records of nectarivorous ant species can be considered nearly complete for the study site. However, only seven ant species were found to attend honeydew-producing homopterans in the rainforest, and no additional trophobiotic ant species were expected based on species richness estimates. All honeydew feeding ant species were also among the EFN visitors. Therefore, the actual use of homopteran honeydew via trophobiotic interactions was obviously limited to a small fraction of the nectarivorous ant species on a local scale, although globally a large proportion of liquid-feeding ant genera was also noted to be trophobiotic (DeVries 1991b, Davidson 1997, Fiedler 2001).

Trophobioses

O. smaragdina ants showed the highest abundance and broadest spectrum of trophobioses **(Chapter 5)**. Despite the polyphagy found for most of the trophobionts attended by this ant, the vast majority (68%) of the trophobiotic feeding sites occurred on two legume liana species (*Entada phaseoloides* and *Caesalpinia traceyi*). Ants were actively involved in the distribution of homopterans, since workers were observed to carry membracid nymphs between aggregations. Locations of these associations were highly dynamic with a mean life-span between 54 days (membracids) and 130 days (coccoids). *O. smaragdina* often sheltered these trophobioses inside leaf pavilions that were stabilised with larval silk.

A special case of ant–plant interactions was found on *Syzygium erythrocalyx* trees which are common at the study site. The tree trunk was regularly inhabited by colonies of *Anonychomyrma gilberti* and thus functioned as a myrmecophyte (see Monteith 1986). The foraging activity of the highly populous ant colonies included many plants in the area surrounding their host tree. *A. gilberti* also foraged on EFNs provided by their host tree and attended cicadellids for honeydew which were highly abundant on its foliage. Therefore, *S. erythrocalyx* showed a key function for the distribution (as nest site) and

nutrition (via nectar and honeydew) of colonies of this dominant ant species **(Chapter 2)**.

O. smaragdina and *A. gilberti* attended most of their trophobionts on tree crowns or canopy lianas. In contrast, all other trophobioses were restricted to the understorey. Honeydew from *A. clerodendri* on understorey shrubs (*C. tracyanum*) was frequently used by two ant species (*Technomyrmex albipes*, *Paratrechina vaga*) which occasionally nested in the leaf galls induced by the aphid **(Chapters 2+4)**. *Crematogaster* cf. *fusca* and *Rhoptromyrmex wroughtonii* attended coccoids on other understorey shrubs.

There was a significant partitioning between ant species and the taxa of trophobionts. This partitioning and the limited ant species spectrum locally involved in trophobioses are likely a product of active competitive exclusion rather than behavioural specialisations between trophobiotic partners, which may be important elsewhere (Seufert & Fiedler 1996, Eastwood & Fraser 1999, Fiedler 2001). When membracids from an *O. smaragdina* colony were offered experimentally to *A. gilberti* workers, they were readily accepted and attended for honeydew although these species were never observed in contact before.

Nectar foraging

While honeydew use was characterised by a high degree of effective specialisation in the associations observed, ant foraging on nectar was generally more opportunistic **(Chapter 2)**. Overlap between ant species and visited plant species was pronounced. Nevertheless, compartmentalisation between species was statistically significant, indicating that plant preferences may vary between ant species, or that some ant and plant species shared a common distribution within the habitat for other reasons.

Sugar baits

The ant assemblage attracted to baits with sugar and amino acid solutions **(Chapter 6)** was generally similar to the ant community consuming natural extrafloral nectar from understorey plants (Chapter 2) (51 vs. 40 species, respectively), including relative abundances of species. This similarity was confirmed by an analysis based on the NNESS index (COMPAH96 software provided by Eugene D. Gallagher). NNESS values between these two assemblages were calculated for the number of plant individuals visited by each ant species to consume extrafloral nectar vs. the number of ant-visited experimental solutions. Resulting values ranged between 0.73 (at parameter $m = 1$, i.e. highest sensitivity for abundant species) and 0.91 ($m = 30$, low

sensitivity for abundant species). Decreased NNESS similarity with increasing influence of abundant species suggests more variable attraction of some abundant species to baits and nectars. In addition, some species were occasionally attracted to baits but not observed on natural nectar sources, in particular ground foraging ants (e.g. *Pheidologeton affinis*, some *Pheidole* spp.). However, most species lacking observations of natural nectar foraging were also uncommon on experimental baits. Therefore, artificial sugar and amino acid solutions proved to be effective in attracting the nectar feeding ant community of the study site in a representative way.

Ant mosaic

The distribution of ant species on nectar and honeydew sources corresponded with the concept of ant mosaics. Ant mosaics have been originally shown for plantations and other secondary tropical habitats (Leston 1970, Room 1971, Majer 1972, Room 1975, Leston 1978, Jackson 1984a, Jackson 1984b, Majer 1993), but rarely investigated in natural rainforests (Dejean & Corbara 2003) where their structural role has been questioned (Floren & Linsenmair 2000). In the present study, the two dominant ant species (*O. smaragdina, A. gilberti*) were mutually exclusive on nectar and honeydew sources **(Chapter 2)**. Battles between colonies from both species were observed and indicate that scrambling competition may be pronounced and correlate with a territorial mosaic. A broad spectrum of ants was commonly associated with *O. smaragdina* on nectar plants. These species regularly used the same trails as the dominant ant (mechanisms involved in such trail-sharing have been discussed elsewhere, see Hölldobler & Wilson 1990, Dejean 1996). Other ant species regularly co-occurred with *A. gilberti* when foraging for nectar. There was a strong and significant separation of these two assemblages, although some species were common in territories of both dominant ants. The same pattern was observed on sugar baits. Both the mutually exclusive distribution of dominant species and their different spectrum of associated hierarchically inferior species have been proposed to characterise ant mosaics (e.g. Majer 1976b).

Co-occurrence

Different ant species regularly co-occurred on the same individual plant, occasionally even on the same leaf without displaying aggressive interactions. For each ant species, the co-occurrence frequency was denoted as the proportion of visited plant individuals **(Chapter 2)** or vial pairs **(Chapter 6)** where simultaneous nectar, honeydew or bait use by other ant or arthropod

species was recorded; restricted to those visits with more than one ant worker per plant. Interspecific variability of such co-occurrences between ants was pronounced. Co-occurrence proportions for baits and for extrafloral and floral nectaries by the same ant species were significantly correlated ($r = 0.54$, $p < 0.05$, $n = 17$ ant species with at least five occurrences each on nectaries and vial pairs). Thus, tolerance of sugar-feeding ants for potential competitors was similar between natural and experimental situations. Co-occurrences were common for many species regularly associated with *O. smaragdina*, while most visits of the dominant ants themselves were characterised by the absence of any other species. The proportion of co-occurrences also varied greatly between plant species and between nectar and honeydew in general, suggesting that tolerance for competitors is a conditional phenomenon which varies with resource quality.

Honeydew and nectar sources not only contrasted in overall diversity and identity of attending ant species, they also showed substantially different visitation patterns on a local scale. While co-occurrences were common among nectar foraging ants, honeydew use on each plant individual was restricted to a single ant colony in all cases observed **(Chapter 2)**. Given that honeydew-feeding ant species were among the most abundant ants at the study site (including the two dominant species that maintain mutually exclusive territories), these observations support earlier studies suggesting that honeydew sources were effectively defended and monopolised by dominant ants, while nectar was used more opportunistically by a broader assemblage (e.g. Schemske 1982, Oliveira & Brandão 1991, Dejean et al. 1997, Blüthgen et al. 2000b).

Dial preferences

Besides ant species partitioning between nectar plant species and trophobiotic homopteran taxa, diet partitioning in other spatio-temporal dimensions were investigated. Ant communities on experimental solutions showed evidence for dial foraging preferences and partitioning (Table 1). Some ants on baits were almost completely diurnal (all *Polyrhachis* spp., *Echinopla australis*, *Leptomyrmex unicolor*, *Crematogaster* sp3); seven common species were significantly more common during diurnal surveys than expected after Bonferroni correction. Six other ant species were significantly overrepresented at night, but none of them was strictly nocturnal.

This dial pattern was less evident for observations at natural resources **(Chapter 2)** where the sample size of observations was more limited than in the experiment. In this dataset, only four species were significantly more common at night (two after Bonerroni correction) and two species during daytime. Dial preferences in four of these species on nectars were the same as on baits, but nocturnal preferences of *Rhoptromyrmex wroughtonii* and *Tetramorium validiusculum* at natural food sources did not recur on experimental baits (Table 1).

Table 1. Most common ant species consuming sugar and amino acid solutions and their visitation parameters. Ant subfamilies: D = Dolichoderinae, F = Formicinae, M = Myrmicinae, P = Ponerinae. Dial activity: diurnal (d) or nocturnal (n) preference deviating significantly from the null hypothesis of homogeneity (chi^2-test, based on number of surveys with and without daylight) (otherwise dn), in brackets when not significant after sequential Bonferroni correction.

Ant species	Subfamily	Dial activity	Ant species (cont.)	Subfamily	Dial activity
Anonychomyrma gilberti	D	d	*Paratrechina minutula*	F	(n)
Camponotus vitreus	F	n	*Pheidole platypus*	M	dn
C. 'nocturnal' (3 spp.) [1])	F	n	*P.* cf. *athertonensis*	M	n
C. sp6 (*gasseri* gp.)	F	n	*Pheidologeton affinis*	M	dn
Crematogaster cf. *fusca*	M	d	*Polyrhachis foreli*	F	d
C. cf. *pythia*	M	dn	*Rhoptromyrmex wroughtonii*	M	dn
C. sp3	M	d	*Rhytidoponera spoliata*	P	(d)
Echinopla australis	F	d	*Tapinoma melanocephalum*	D	d
Leptomyrmex unicolor	D	dn	*Technomyrmex albipes*	D	(n)
Monomorium floricola	M	d	*Tetramorium insolens*	M	n
Oecophylla smaragdina	F	(d)	*T. validiusculum*	M	dn
Paratrechina vaga	F	n			

Canopy vs. understorey

Vertical stratification of ant species foraging for nectar was significant **(Chapter 2)**. Several species including the two dominant ants *O. smaragdina* and *A. gilberti* were much more common on nectar sources in the canopy, although no true canopy specialists were found among species that were regularly sampled. In contrast, about half of the species recorded on nectar sources only occurred on understorey plants, suggesting that canopy foraging was restricted to a subset of the entire fauna (including species with nest locations in the canopy or near the ground).

Conclusions about community patterns

Bottom-up effects and competition

The resource partitioning found for ants between nectar and honeydew sources is a strong indication that bottom-up effects are important in tropical ant communities. In addition, interspecific competition between ants was pronounced and highly asymmetrical (see also Fellers 1987, Savolainen & Vepsäläinen 1988, Andersen 1992). Competitive hierarchies were associated with resource defence through territorial behaviour and generated ant mosaic structures. Spatio-temporal compartmentalisation (dial patterns, stratification) may be one mode of diet partitioning that is associated with reduced interspecific competition between ants. However, turnover between diurnal and nocturnal assemblages was limited (albeit significant) compared to some other nectarivorous or trophobiotic ant communities reported elsewhere (Del-Claro & Oliveira 2000, Hossaert-McKey et al. 2001). Furthermore, vertical stratification was not as pronounced as in other ant communities from tropical forests (Longino & Nadkarni 1990, Brühl et al. 1998). Stratification was characterised by interspecific variation in relative abundance in the canopy vs. understorey rather than true canopy specialisation, although many species were never observed to forage in the canopy. The following analysis of resource composition and preferences aimed to detect whether nectar quality measures, instead of spatio-temporal partitioning, can be linked to differential resource use by ants.

Processes – Diet composition and preferences

Nectar and honeydew composition

Sugar and amino acid profiles

Nectar and honeydew sources showed a great variability in sugar and amino acid composition **(Chapter 3)**. Most nectars were dominated by the three carbohydrates sucrose, glucose and fructose. Honeydew contained various other sugars, and the trisaccharides melezitose and raffinose were highly concentrated in some sources.

Among the amino acids, proline, alanine and threonine were found in most nectar and honeydew samples, while others such as glycine, methionine and cysteine were relatively rare. In total, 17 α-amino acids were identified from these sources. The similarity of amino acid profiles was compared using ordination statistics (Figure 1).

Following this method, extrafloral nectars, floral nectars and honeydew sources show a large overlap in amino acid composition.

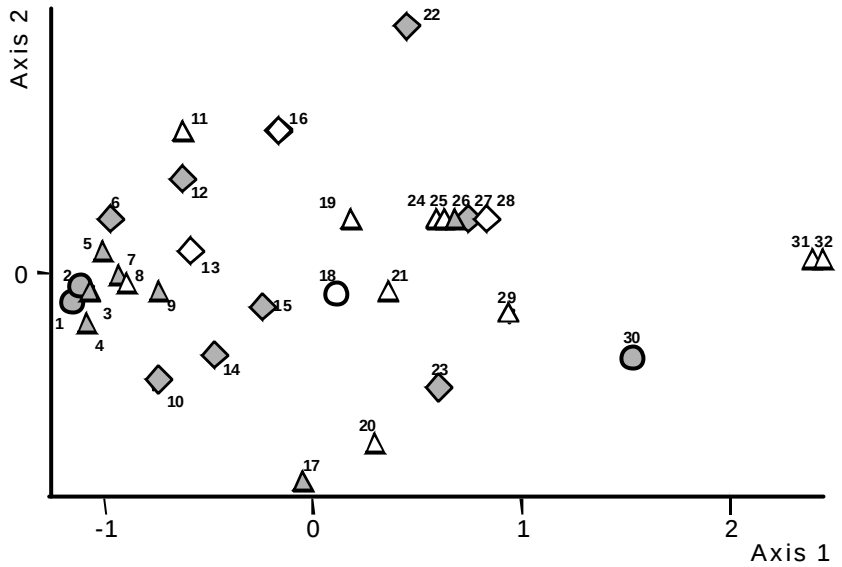

Fig. 1. Ordination of amino acid profiles obtained by nonmetric multidimensional scaling (NMDS) based on Sörensen similarity index (two dimensions were selected, stress 0.10) (software used: Community Analysis Package 2.04, Pisces Conservation Ltd.). Extrafloral nectar (triangles), floral nectar (diamonds), and honeydew sources (circles) were distinguished [1]), resources used by *Oecophylla smaragdina* ants were marked grey. Overlapping symbols had the same coordinates.

[1]) Number code: 1 *Sextius* '*kurandae*' on *Caesalpinia traceyi*, 2 *S.* '*kurandae*' on *Entada phaseoloides*, 3 *Flagellaria indica*, 4 *Smilax* cf. *australis*, 5 *Adenia heterophylla*, 6 *E. phaseoloides*, 7 *Macaranga involucrata*, 8 *Aleurites rockinghamensis*, 9 *Syzygium erythrocalyx*, 10 *Cryptocarya murrayi*, 11 *Ardisia pachyrrhachis*, 12 unidentified liana, 13 *Normanbya normanbyi* pistill, 14 *N. normanbyi* flower base and wound sap, 15 *Cryptocarya hypospodia*, 16 *Syzygium gustavioides*, 17 *Merremia peltata*, 18 Idiocerinae on *S. erythrocalyx*, 19 *E. phaseoloides*, 20 *Endospermum myrmecophilum*, 21 *Macaranga tanarius*, 22 *Licuala ramsayi*, 23 *Elaeocarpus angustifolius*, 24 *Dysoxylum pettigrewianum*, 25 *Homalanthus novoguineensis*, 26 *Cardwellia sublimis* wound sap, 27 *Dysoxylum papuanum*, 28 *Dysoxylum mollissimum*, 29 *Clerodendrum tracyanum*, 30 *Milviscutulus* on *Melodinus australis*, 31 *Ipomoea indica*, 32 *Melicope elleryana* (see Chapter 3 for details).

Four sources were recognised where none or only one of the 17 focal amino acids was missing **(Chapter 3)**. These cases were: (1) honeydew samples collected from *Sextius* '*kurandae*' membracids on *E. phaseoloides* or (2) *C. traceyi* lianas, (3) EFN from *Flagellaria indica* or (4) *Smilax* cf. *australis*. These honeydew sources (1-2) were exclusively used by *O. smaragdina* ants. They represented the most common trophobiotic associations of this ant at the study site. Furthermore, per capita ant recruitment to homopterans on these two legume liana species was significantly higher than on other plants **(Chapter 5)**. This may be indicative of a higher honeydew production or honeydew quality

on these hosts, where the richness of amino acids may be an important factor. The two EFN plant species (3-4) were also most commonly attended by *O. smaragdina* and often found to be monopolised by these dominant ants. Ant species co-occurrences on both EFNs were significantly less common than expected **(Chapter 2)**, while co-occurrences were more common on many extrafloral and floral nectars that were poorer in amino acids.

Resource preferences

A discriminant analysis was used to model associations between amino acid and sugar characteristics and ant species visitation. Resources used by the dominant *O. smaragdina* (Table 2) were significantly predicted by similar amino acid profiles and high total sugar concentration. They generally tended to have a higher sucrose:hexose concentration ratio, higher total amino acid concentration and higher diversity of amino acids, but those individual factors were not significant. None of the other ant species showed significant discrimination in the overall model. Hence, only the competitively superior species *O. smaragdina* demonstrated pronounced preferences for sugar and amino acid traits through its selection among natural nectar and honeydew sources.

Table 2. Discriminant analysis modeling the explanatory power of six sugar and amino acid characteristics to explain nectar foraging of *Oecophylla smaragdina* at natural food sources. Mean factor values ± standard error shown for resources used vs. not used by this ant, respectively. Amino acid profiles were quantified as the first two dimensions of the NMDS ordination (Figure 1). Significant results marked in bold (software used: Statistica 5.5, StatSoft Inc.).

Discriminant factor	Used (n = 19)	Not used (n = 13)	$F_{1, 25}$	p
Amino acid profiles: NMDS axis 1	-0.31 ± 0.19	0.45 ± 0.29	**5.11**	**0.03**
Amino acid profiles: NMDS axis 2	-0.03 ± 0.07	0.05 ± 0.08	2.31	0.14
Total sugar concentration [g/l]	396 ± 64	181 ± 42	**5.10**	**0.03**
Sucrose/(Sucrose+Hexose)	0.6 ± 0.1	0.3 ± 0.1	1.73	0.20
Total amino acid concentration [g/l]	5.5 ± 1.8	0.7 ± 0.2	1.42	0.24
Number of amino acids	7.7 ± 1.0	4.9 ± 0.9	1.19	0.29
Whole model	Wilks' λ = 0.49, $F_{6, 25}$ = **4.36**, p = **0.004**			

Sugar and amino acid preferences

Sugar preferences

In order to assess the impact of resource composition and interspecific competition on dietary preferences of ants, controlled experiments using artificial sugar and amino acid solutions were performed **(Chapter 6)**. These

tests revealed variable gustatory preferences among ant species. Most common ant species preferred 15% (w/w) sucrose solutions over solutions of other single carbohydrates in the same concentration. Even the dominant honeydew trisaccharides melezitose and raffinose were not more attractive to any of the ant species than sucrose, in contrast to reports for European *Lasius niger* ants (Duckett 1974, Völkl et al. 1999, Tinti & Nofre 2001) that have led to speculation about a general ant-attracting role of melezitose in honeydew (Kiss 1981). Many ant species preferred glucose over fructose, although *A. gilberti* showed the opposite choice. The attractiveness of solutions to ants also increased with higher sugar concentrations.

Amino acid preferences

Sugar solutions containing mixtures of amino acids were usually preferred over pure sugar solutions (supporting earlier findings by Lanza & Krauss 1984, Lanza 1988, 1991, Lanza et al. 1993), although some species showed no significant selectivity or even discrimination against some amino acid mixtures. A completely different picture was found for the ants' selection of single amino acids in sugar solutions. In numerous cases, certain ant species showed significant preferences of one amino acid over another, while different ant species performed a significant opposite choice. The two dominant ants *O. smaragdina* and *A. gilberti* differed substantially in their preferences. This interspecific variability in gustatory preferences may be caused by different taste reception or physiological requirements. For recognition of at least some amino acids, synergetic effects with sugars may be important. Phenylalanine and asparagine, highly attractive to *O. smaragdina* or *A. gilberti* when offered in sugar solutions, respectively, were not discriminated against water controls when solved without sugar. Such synergistic effects have been studied in detail for glycine and glucose taste reception in *Camponotus japonicus* (Wada et al. 2001).

Conditional effects on preferences

However, gustatory preferences among sugars and amino acids by each ant species or colony were not fixed and stereotypical, but subject to conditional effects. After ant colonies had been feeding large amounts of a preferred amino acid solution for two days, their attractiveness was significantly reduced. Therefore, previous experience or changes in colony requirements may be involved in foraging decisions. Moreover, the preferences expressed in the absence of other species were often significantly reduced when two or more

species co-occurred on the same baits. This observation indicates an effective influence of interspecific competition on the ants' dietary choices. Conditional changes were found both for sugar and amino acid preferences of ants; such conditionality in foraging decisions by nectarivores has been rarely demonstrated previously (but see Pimm et al. 1985, Sandlin 2000).

Trophic diversity in ant communities

Nutritional importance of plant derived resources

The availability and composition of nectar or honeydew sources turned out to be a significant factor influencing the ant community structure, implying that such plant sap sources play an important role in the nutrient and energy budget of the ant colonies involved. The fundamental importance of plant exudates has also been hypothesised based on the fact that the biomass of ants in rainforest canopies often exceeds the biomass of other arthropods that could provide potential prey (Tobin 1991, 1994, 1995). However, most ant species are omnivores (Stradling 1978) consuming various diets, and classical methods to determine the relative contribution of prey vs. plant sap sources to the nourishment of ants are difficult and problematic. In the present study, stable isotope techniques have been used to unravel the trophic positions of 50 ant species **(Chapter 7)**. The composition of carbon and nitrogen isotopes of ant workers were analysed and showed a great variability between species. Largely ground-foraging and highly predacious taxa (*Aenictus atratus*, Ponerinae, some *Pheidole* spp.) were characterised by high concentrations of heavy nitrogen (^{15}N). On the contrary, arboreal ants that frequently consumed nectar had the lowest ^{15}N concentrations, and extreme cases were effectively indistinguishable in their ^{15}N signature from true herbivores. Ant species were continuously distributed along a ^{15}N concentration gradient that has been interpreted as an indicator of trophic position in other food webs (Peterson & Fry 1987, Ponsard & Arditi 2000, Scheu & Falca 2000, Post 2002b). Variation in ^{15}N corresponds with assumptions of the ants' diets based on feeding observations from the study site or evidence from the literature (Shattuck 1999). Carbon isotopes were less informative about trophic positions, which was also reported from other studies (Ponsard & Arditi 2000). Interspecific variability in nitrogen isotopes was significant and independent of plant substrate variability. The dominant ants *O. smaragdina* and *A. gilberti* had intermediate ^{15}N levels. Both ant species were highly predatory as well as

feeding on nectar and honeydew. Despite their higher trophic position indicated by nitrogen isotopes, their large colonies maintained the largest trophobiotic associations found at the study site and they were among the three most common nectar visitors **(Chapter 2)**.

Trophic plasticity

Isotope composition also differed markedly between colonies of *O. smaragdina*, where colonies from open secondary vegetation had significantly higher ^{15}N levels than from mature forests. Most of the preferred nectar sources and host plants of associated homopterans were more common in, or completely restricted to, mature forests stages **(Chapter 2+5)**. Pioneer plants in secondary vegetation (e.g. shrubs of Euphorbiaceae) often attracted ants to extrafloral nectaries, but rarely *O. smaragdina*. This may be correlated with the pronounced selectivity in nectar foraging displayed by this ant species (Table 2), since extrafloral nectar from most euphorbs was relatively poor in amino acids and low in sugar concentration. Therefore, the plasticity in trophic positions of *O. smaragdina* colonies indicated by ^{15}N levels may be triggered by the availability of suitable high-quality nectar and honeydew sources. Lacking these, weaver ants may express a higher degree of predation.

Nitrogen flow from nectar

The enrichment of ^{15}N along the trophic food chain as indicated in the present analysis of the ant community also suggests that nitrogen fluxes from nectar to nectarivores and from honeydew to trophobionts is important. Nitrogen availability is often a limiting factor in animal fitness, which may be true in particular for canopy ants (Davidson 1997, Yanoviak & Kaspari 2000). Amino acids are usually the most prevalent source of nitrogen in nectars (Baker & Baker 1973, 1983) and honeydew (Auclair 1963). Therefore it may not be surprising that amino acids play a central role in dietary preferences and foraging decisions of ants **(Chapter 6)**.

Conclusions about processes regulating resource use

Diet partitioning and competition

The results indicate that nectar and honeydew source partitioning between ants may be driven by three factors: (a) strong asymmetrical competitive interactions within the community, (b) variation in nectar composition preferences mediated by taste and physiological requirements, and (c) some degree of spatio-temporal differentiation including stratification, dial preferences and plant species preferences.

Among extrafloral and floral nectar sources, competitively superior weaver-ants (*Oecophylla smaragdina*) were more selective for sugar and amino acid traits than the rest of the community. Nectars preferred by *O. smaragdina* were characterised by higher sugar and amino acid concentration, higher sucrose:hexose ratio and similar composition of amino acids. In the absence of competition during cafeteria experiments, however, most ant species preferred artificial sugar solutions containing amino acids over pure sugar solutions, and sucrose over most other carbohydrates. Preferences for single amino acids were highly species-specific and idiosyncratic. In the presence of competitors, nectar preferences were reduced. Thus ecological and physiological optima may differ, particularly in competitively inferior ants. In general, amino acids derived from nectar or honeydew may hold a key function in resource preferences and resource defence of ants, and they are an important source of nitrogen for a broad spectrum of omnivorous ants.

Summary

Ant communities visiting nectar and honeydew sources were studied in a tropical lowland rainforest in North Queensland, Australia, using a canopy crane facility to access the upper forest stratum. The study focused on the hypothesis whether the distribution and composition of nectar and honeydew diets influence resource partitioning and competition in the ant community, and thus regulate community composition.

Ants were the most common consumers on all extrafloral nectaries, while they constituted only a minority of floral visitors. In total, 43 ant species were observed to consume nectar from extrafloral nectaries (34 plant species) or from flowers (14 plant species). Extrafloral nectaries were found on 17% of the tree species and 21% of the climbing plant species of the study site. Ants also consumed wound sap exudates on three plant species. Six nectar-foraging ant species attended trophobionts for honeydew. Trophobiotic partners included homopterans from at least 12 species of eight families (Aphidae, Coccidae, Cicadellidae, Eriococcidae, Diaspididae, Margarodidae, Membracidae, Pseudococcidae) and two species of lycaenid caterpillars. Detailed studies were performed on the spatio-temporal dynamics of trophobioses of *Oecophylla smaragdina* ants and the general distribution of trophobioses involving the aphid *Aphis clerodendri*. Species accumulation curves indicate a near-complete coverage of the local ant fauna attracted to nectaries or trophiobionts at the study site.

Ant species showed a significant compartmentalisation of nectar use across plant species, although most ant species visited a broad spectrum of plants that strongly overlapped between different ants. Trophobioses were much more specialised at the study site, and some ant species attended certain trophobionts exclusively.

On each plant individual, only a single ant colony was observed attending trophobionts. In contrast, simultaneous co-occurrences between different ant species foraging for nectar on the same plant individuals were common (observed in 23% of the surveys), although these proportions varied strongly across plant and ant species. The two most dominant ant species (*O. smaragdina* and *Anonychomyrma gilberti*) had mutually exclusive territories, and they were each associated with a significantly different assemblage of other ant species on nectar plants. This community pattern corresponds with the concept of ant mosaics that is based on dominance hierarchies. The ant community showed a significant vertical

stratification and dial preferences, although neither completely nocturnal species nor true canopy specialists were found, unlike in other studies.

Honeydew and nectar sources varied substantially in carbohydrate and amino acid concentration and composition as revealed by HPLC analyses. Sucrose, glucose and fructose were the most common sugars in most sources, while maltose, melibiose, lactose, melezitose and raffinose were common only in honeydew and rare or absent in nectars. Seventeen α-amino acids were identified, among which proline, alanine and threonine were the most common ones.

There was a strong relationship between the composition of honeydew and nectar sources and their use by ants, in particular by the dominant *O. smaragdina*. Among all 32 nectar and honeydew sources analysed, resources actually consumed by this ant were characterised by relatively similar amino acid profiles and higher total sugar concentration. The most common diets of *O. smaragdina* included two honeydew sources (*Sextius* '*kurandae*' membracids on *Entada phaseoloides* and *Caesalpinia traceyi* legume lianas) and two extrafloral nectars (*Flagellaria indica* and *Smilax* cf. *australis*) that had the broadest spectrum of amino acids, containing 16 or all 17 of those amino acids identified. These two honeydew sources represented 64% of the total trophobiotic aggregation sites found with this ant. Furthermore, trophobioses on lianas showed a significantly higher per capita recruitment of this ant species (number of workers per individual homopteran) compared to trees. *F. indica* and *S.* cf. *australis* extrafloral nectaries were also commonly monopolised by *O. smaragdina* in a similar way as trophobioses; co-occurrences were significantly rarer than at other nectar sources.

Field experiments on nectar preferences were performed using artificial sugar and amino acid solutions in pairwise comparisons. The community attracted to these solutions (51 ant species) was very similar to the ant community observed at real nectar sources. Preferences among sugars were largely concordant between ant species. For most ant species, sucrose was more attractive than any other sugar, and attractiveness increased with sugar concentration. Most ant species also preferred sugar solutions containing mixtures of amino acids over pure sugar solutions. However, choices between different single amino acids in sugar solutions varied substantially and significantly between species. Preferences between solutions were significantly reduced in the presence of competing ant species. Thus the experiments show that both variability in gustatory preferences, especially for amino acids, and conditional effects of competition may be important for resource selection and partitioning in nectar feeding ant communities.

Stable carbon and nitrogen isotope composition was analysed for 50 ant species, and additionally for associated plants, homopterans and other arthropods from the study site. Ant species differed strongly and significantly in isotope signatures. Nitrogen isotope ratios ($\delta^{15}N$) of ants were not correlated with those of plant foliage from which the ants were collected. Instead, $\delta^{15}N$ may represent a powerful indicator of trophic position of omnivorous ants like in other foodweb studies, suggesting that members of the ant community spread out in a continuum between largely herbivorous species, feeding on nectar or honeydew, and predatory taxa. Variability between colonies of the same species was also pronounced. $\delta^{15}N$ values of *O. smaragdina* colonies from mature forests, where most of their nectar and honeydew sources are found, indicate lower trophic levels than isotope signatures of colonies from open secondary vegetation.

This study demonstrates that the distribution and quality of honeydew and nectar sources have a strong structuring impact in diverse tropical ant communities. Amino acids were found to play a key role for ant species preferences and competition, and for nitrogen fluxes to colonies of the arboreal ant fauna.

Zusammenfassung

In dieser Arbeit wurden Ameisengemeinschaften an Nektar- und Honigtauquellen in einem tropischen Tieflandregenwald in Nord-Queensland, Australien, untersucht. Die oberen Kronenschichten des Waldes konnten mit Hilfe eines Kranes in die Untersuchungen einbezogen werden. Die zentrale Hypothese dieser Arbeit war, ob die Verteilung und die Zusammensetzung von Nektar und Honigtau die Ressourcenpartitionierung und Konkurrenz in der Ameisengemeinschaften beeinflusst und daher die Zusammensetzung der Gemeinschaft reguliert.

Ameisen stellten die häufigsten Besucher aller extrafloraler Nektarien, aber nur einen geringen Anteil der Blütenbesucher dar. Insgesamt wurden 43 Ameisenarten beobachtet, die Nektar an extrafloralen Nektarien (34 Pflanzenarten) und Blüten (14 Pflanzenarten) konsumierten. Extraflorale Nektarien wurden bei 17% der Baumarten und 21% der Kletterpflanzen des Untersuchungsgebiet nachgewiesen. Darüber hinaus nutzten Ameisen an Pflanzenwunden austretende Säfte bei drei Pflanzenarten. Von den 43 nektarivoren Ameisenarten traten sechs Arten als Nutzer von Honigtau in trophobiotischen Assoziationen auf. Trophobiosepartner umfassten mindestens 12 Homopterenarten aus acht Familien (Aphidae, Coccidae, Cicadellidae, Eriococcidae, Diaspididae, Margarodidae, Membracidae, Pseudococcidae) und zwei Bläulingsraupen-Arten (Lycaenidae). Detaillierte Studien wurden zur raum-zeitlichen Dynamik der Trophobiosen von *Oecophylla smaragdina* Ameisen und zur generellen Verbreitung der Trophobiosen der Blattlaus *Aphis clerodendri* durchgeführt. Arten-Akkumulationskurven deuten auf eine nahezu komplette Erfassung der lokalen Ameisenfauna an Nektarien und Trophobiosen des Untersuchungsgebietes hin.

Die nektarivoren Ameisengemeinschaften verschiedener Pflanzenarten unterschieden sich signifikant, obwohl alle regelmäßig erfassten Ameisenarten ein breites und stark überlappendes Spektrum an Pflanzenarten nutzten. Hingegen zeigten Trophobiosen einen stärkeren Grad an Spezialisierung im Untersuchungsgebiet; einige Ameisenarten waren exklusiv mit bestimmten Trophobionten assoziiert.

An den Trophobiosen eines Pflanzenindividuums trat in sämtlichen beobachteten Fällen nur jeweils eine einzige Ameisenkolonie auf. Pflanzenindividuen mit Nektarien wurden dagegen häufig von mehreren Ameisenarten gleichzeitig genutzt (bei 23% der Beobachtungen), wobei dieser Anteil für verschiedene Pflanzenarten und Ameisenarten

stark variierte. Territorien der beiden dominanten Ameisenarten (*O. smaragdina* und *Anonychomyrma gilberti*) zeigten keine Überschneidungen. Beide Arten waren an Nektarquellen jeweils mit einem signifikant unterschiedlichen Artenspektrum an Ameisen assoziiert. Dieses Muster stimmt mit dem Konzept der Ameisen-Mosaike überein, das auf Dominanzhierarchien basiert. Die Ameisengemeinschaft zeigte in ihrer Ressourcennutzung eine signifikante vertikale Stratifikation und tageszeitliche Präferenzen. Allerdings wurden weder rein nachtaktive Arten, noch echte Kronenraumspezialisten gefunden, im Gegensatz zu einigen Studien aus anderen Regionen.

Honigtau- und Nektarquellen zeigten eine ausgeprägte Variabilität in der Konzentration und Zusammensetzung von Zuckern und Aminosäuren. Die häufigsten Zucker waren Saccharose, Glukose und Fruktose. Darüber hinaus traten Maltose, Melibiose, Laktose, Melizitose und Raffinose in Honigtau häufig, in Nektar dagegen selten oder gar nicht auf. Siebzehn α-Aminosäuren wurden identifiziert, wobei Prolin, Alanin und Threonin am häufigsten auftraten.

Die Zusammensetzung der Honigtau- und Nektarquellen zeigte einen deutlichen Zusammenhang mit ihrer Nutzung durch Ameisen, insbesondere der dominanten *O. smaragdina*. Von 32 analysierten Nektar- und Honigtauquellen waren die von dieser Ameisenart tatsächlich genutzten Ressourcen durch relativ ähnliche Aminosäureprofile und eine höhere Zuckerkonzentration charakterisiert. Zu den häufigsten Futterquellen von *O. smaragdina* zählten zwei Honigtauquellen (*Sextius 'kurandae'* Buckelzirpen an Lianen der Leguminosenarten *Entada phaseoloides* und *Caesalpinia traceyi*) und zwei extraflorale Nektarquellen (*Flagellaria indica* und *Smilax* cf. *australis*), welche jeweils die höchste Anzahl von Aminosäuren (16 oder sämtliche 17 der identifizierten Aminosäuren) aufwiesen. Diese Honigtauquellen repräsentierten 64% der Aggregationsstellen von Trophobiosen dieser Ameisenart. Trophobiosen an Lianen zeigten außerdem eine signifikant höhere Rekrutierungsrate von *O. smaragdina* (Zahl der Arbeiterinnen pro Homopteren-Individuum) als an Bäumen. Auch die extrafloralen Nektarien von *F. indica* und *S.* cf. *australis* wurden von *O. smaragdina* häufig in ähnlicher Weise wie die Trophobiosen monopolisiert; gleichzeitiges Auftreten verschiedener Ameisenarten wurde signifikant seltener beobachtet als bei den übrigen Nektarquellen.

Freilandexperimente zu Nektarpräferenzen wurden mit künstlichen Zucker- und Aminosäuregemischen in paarweisen Tests durchgeführt. Die Ameisengemeinschaft an diesen künstlichen Lösungen (51 Arten) war der Nutzungsgemeinschaft an echten Nektarien sehr ähnlich. Zuckerpräferenzen wiesen eine hohe Übereinstimmung zwischen

Ameisenarten auf. Saccharose wurde von den meisten Arten gegenüber anderen Zuckern bevorzugt, und die Attraktivität der Zuckerlösungen stieg mit ihrer Konzentration. Die meisten Arten bevorzugten außerdem Zuckerlösungen mit einem Gemisch aus Aminosäuren gegenüber reinen Zuckerlösungen. Im Gegensatz dazu zeigten die Präferenzen für verschiedene einzelne Aminosäuren in Zuckerlösungen substanzielle und signifikante Unterschiede zwischen Ameisenarten. Präferenzen waren außerdem signifikant reduziert in Gegenwart konkurrierender Ameisenarten. Diese Experimente deuten einerseits auf den Einfluss geschmacksphysiologischer Unterschiede zwischen den Ameisenarten, insbesondere bei Aminosäuren, für die Selektion und Partitionierung von Ressourcen in nektarivoren Ameisengemeinschaften hin. Andererseits sind auch die Auswirkungen von Konkurrenz von entscheidender Bedeutung.

Von 50 Ameisenarten wurde die Zusammensetzung stabiler Kohlenstoff- und Stickstoffisotope analysiert, außerdem für Pflanzen, Homopteren und andere Arthropoden des Untersuchungsgebietes. Die Ameisenarten zeigten ausgeprägte und signifikante Unterschiede in ihren Isotopensignaturen. Die Zusammensetzung von Stickstoffisotopen ($\delta^{15}N$) bei Ameisen war dabei nicht mit den Werten der Blätter von Pflanzen korreliert, von denen die Ameisen gesammelt wurden. Stattdessen wird angenommen, dass $\delta^{15}N$-Werte Indikatoren für die jeweilige trophische Position der omnivoren Ameisen darstellen, vergleichbar mit anderen Studien von Nahrungsnetzen. Die Ergebnisse deuten darauf hin, dass in dieser Gemeinschaft ein Kontinuum von größtenteils herbivoren Arten, die Nektar und Honigtauquellen nutzen, bis hin zu räuberischen Arten vorliegt. Neben interspezifischen Unterschieden war außerdem die Variabilität verschiedener Kolonien derselben Ameisenart sehr ausgeprägt. Bei *O. smaragdina* deuten $\delta^{15}N$-Werte von Kolonien in geschlossenen Waldstadien, in denen die meisten ihrer Nektar- und Honigtauquellen vorkommen, auf niedrigere Trophieebenen hin im Vergleich zu Kolonien in offener Sekundärvegetation.

Diese Arbeit belegt, dass die Verteilung und Qualität von Nektar und Honigtauquellen einen starken strukturierenden Einfluss auf artenreiche tropische Ameisengemeinschaften haben. Aminosäuren haben dabei eine Schlüsselfunktion für Präferenzen und Konkurrenz, sowie für den Stickstoffhaushalt von Kolonien der arborealen Ameisenfauna.

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Hiermit erkläre ich, daß ich die vorliegende Arbeit selbständig verfaßt und dabei keine anderen als die hier angegebenen Quellen und Hilfsmittel verwendet habe.

Ferner erkläre ich, daß ich diese Arbeit weder einer anderen Prüfungsbehörde vorgelegt noch anderweitig mit oder ohne Erfolg versucht habe, eine Dissertation einzureichen oder mich der Doktorprüfung zu unterziehen.

Bayreuth, den 9. April 2002

Nico Blüthgen