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Disentangling a rainforest food web using stable isotopes: dietary diversity in a species-rich ant community

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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 hyperdominance of ants in tropical tree crowns, where prey organisms tend to occur scarcely and unpredictably. We therefore examined N and C stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) 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 $\delta^{15}\text{N}$ and 6.8‰ in $\delta^{13}\text{C}$). Isotope signatures of the entire ant community overlapped with those of several herbivorous as well as predacious arthropods. Variability in $\delta^{15}\text{N}$ between ants was not correlated with plant $\delta^{15}\text{N}$ 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’ $\delta^{15}\text{N}$ were consistent with the trophic level predicted by natural feeding observations, but not their $\delta^{13}\text{C}$. Low $\delta^{15}\text{N}$ levels were recorded for ant species that commonly forage for nectar on understorey or canopy plants, intermediate levels for species with large colonies that were highly abundant on nectar and honeydew sources and were predacious, and the highest levels for predominantly predatory ground-foraging species. Colonies of the dominant weaver-ants

(*Oecophylla smaragdina*) had significantly lower $\delta^{15}\text{N}$ in mature forests (where preferred honeydew and nectar sources are abundant) than in open secondary vegetation. N 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.

Keywords Honeydew · Nectar · Omnivory · Trophic levels · Tropical forest canopy

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 and 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, obtaining such observational evidence is difficult and time-consuming. 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 the stable isotope composition of organisms provides an alternative approach. As a consequence of isotopic fractionation associated with many physiological processes, isotope signatures give 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

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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 and Arditi 2000; Scheu and 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 and 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 and Wilson 1990). The dominance of ants in tropical forest canopies has led to the prediction that canopy ants must gain most of their nutrient requirements as primary consumers (nectar and honeydew) rather than through predation (Tobin 1991; Davidson 1997). Recent observations, supported by modern methods of access to the tree crowns, indicated that most rainforest canopy ant species indeed feed extensively on honeydew and nectar besides prey (Blüthgen et al. 2000; 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 N-poor plant exudates could be sufficient to sustain the nutrient 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 that quite variable proportions of C are obtained directly from plants (Fisher et al. 1990; Rico-Gray and 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 one can extrapolate from these results to give an impression of entire communities. On the ant community level, it remains practically unknown how species are partitioned across the isotopic landscape. Preliminary analyses of N 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 and 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 (Blüthgen and Fiedler 2002, Blüthgen 2003). Our analysis included 50 ant species active in the canopy, understory and on the ground (but excluding the soil fauna), associated homopterans and plants. Specifically, we addressed the question whether C and N 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 those of homopterans. We also examined whether ants (species or colonies) are partitioned between distinct trophic levels (trophic specialization) or continuously distributed between them (omnivory).

Materials 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. 3 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 years of age, dominated by *Macaranga tanarius*. The annual rainfall is ca. 3,500 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 ten *Oecophylla smaragdina* workers collected while attending homopterans had on average 0.7‰ lower $\delta^{13}\text{C}$ and 0.9‰ lower $\delta^{15}\text{N}$ values than the remaining body; the C:N ratio was nearly doubled ($n=2$ comparisons from different colonies, each comprising five workers). Thus, exclusion of ant gasters was deemed necessary to obtain an unbiased measure of the 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. nine different colonies, and a further 16 species by three colonies each to enable us to recognize intraspecific variability. Each sample contained typically ten workers from the same colony, but often fewer or more depending on availability and size (between one and 30). The coefficient of variation (CV) between three individuals from the same colony was examined for one colony of *O. smaragdina* ($\delta^{13}\text{C}$, CV=1.3%; $\delta^{15}\text{N}$, CV=5.2%) and one of *A. gilberti* (0.7%, 18.4%). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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, intracolony 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 disregarded ant sexuals. Larvae and/or pupae were collected from 12 nests of 11 species and major and minor worker castes separately from eight colonies of seven 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 modelling, 11 different arthropods were sampled from plants (Araneae: Thomisidae; Blattodea; Diptera; Heteroptera; Hymenoptera: Apidae; Isopoda; Ensifera: Tettigoniidae; Mantodea; Phasma-

toidea; Coleoptera: Brentidae; Lepidoptera) and from the ground (Ensifera: Gryllotalpidae).

Plant samples included 13 common species of canopy trees, five species of climbing plants, two palms and five understorey shrubs (total 37 plant individuals). These samples represent plant species commonly visited by ants for extrafloral and floral nectar or honeydew-producing homopterans (Blüthgen 2003) and/or characteristic canopy trees that hosted *O. smaragdina* colonies (Blüthgen and Fiedler 2002). From all plant species in the canopy, 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 one to two individuals in the analysis. Analyses across species of ants, plants or homopterans are based on species means, for which all samples from each species were averaged.

Isotopic analysis

Samples were weighed on an electronic balance (Sartorius M25D, Göttingen, Germany) and placed in tin capsules (for samples >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, Milan; ConFlo III interface and gas-IRMS delta S, both Finnigan MAT, Bremen). The deviation of the sample from the international standard in per mil (‰) is expressed as: $\delta^{13}\text{C}$, $\delta^{15}\text{N}(\text{‰}) = (R_{\text{sample}}/R_{\text{standard}} - 1) \times 10^3$, where R_{sample} denotes the ratio between the heavy isotope and its lighter counterpart ($R_{\text{sample}} = {}^{13}\text{C}/{}^{12}\text{C}$, or ${}^{15}\text{N}/{}^{14}\text{N}$) 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 standards (Gebauer and 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 $\pm 0.15\text{‰}$ or better. Reproducibility was routinely controlled by measurement of acetanilide (Merck, Germany). Acetanilide was furthermore used to calibrate C and N concentration measurements (Gebauer and Schulze 1991).

Data analysis

In order to compare isotope data with observations on ant feeding behaviour, we used observations of ant species feeding on nectar and honeydew from the study site between 1999 and 2002 (data in Blüthgen 2003). 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 (Blüthgen 2003). 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 MANOVA for both variables $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. In case of significance, univariate tests of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were performed. Isotope data did not deviate significantly from the 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 $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ between ant species is not significantly larger than expected (Ponsard and Arditi 2000). Expected values are variances in trophic enrichment (Δ) of animals compared to their diet: $\sigma^2_{\Delta}(\delta^{13}\text{C}) = 1.96\text{‰}$, $n=76$ and $\sigma^2_{\Delta}(\delta^{15}\text{N}) = 1.21\text{‰}$, $n=26$ (Gearing et al. 1984; Mingawa and Wada 1984; Ponsard and Arditi 2000). The test is considered conservative since variability of fractionation within a single taxon (ants) is probably smaller than between various vertebrates and invertebrates considered by the above studies. In addition, bulked samples of ant workers from the same colony may reduce isotopic variance (but note that bulking varied between species).

Results

Plants

Leaf samples (species listed in the Appendix) showed some variation in isotope signatures (mean \pm SD, range, $\delta^{13}\text{C} = -28.5 \pm 1.7\text{‰}$, -26.3 to -31.4‰ ; $\delta^{15}\text{N} = 2.2 \pm 1.3\text{‰}$, 0.2 – 4.9‰ , $n=25$ species means; Fig. 1a). Variability between conspecific plants was high (see Fig. 1a), particularly for $\delta^{15}\text{N}$ in *Syzygium erythrocalyx* (range 0.2 – 4.2 , $n=5$). Across species, samples from the two sites did not differ in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (MANOVA, Rao's $R_{2,24} = 0.21$, $P = 0.81$, $n_{\text{site-1}} = 21$, $n_{\text{site-2}} = 6$ species means), and no difference was found between samples from mature forests at both sites vs. young secondary forest at site-2 ($R_{2,24} = 0.18$, $P = 0.83$, $n_{\text{mature}} = 22$, $n_{\text{young}} = 5$). 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 ($\delta^{15}\text{N}$, Pearson's $r = 0.79$, $P < 0.001$; $\delta^{13}\text{C}$, $r = 0.56$, $P = 0.01$, $n = 20$ sample pairs) (dotted lines in Fig. 1a). In membracids and cicadellids (both Auchenorrhyncha), all samples except one were more enriched in ${}^{13}\text{C}$ than their host plant foliage (mean difference to host plant \pm SD $1.7 \pm 1.1\text{‰}$, range -0.3 to 2.7‰ , $n = 9$). The ${}^{15}\text{N}$ concentration of cicadellids was consistently above the plant level (mean difference 0.7 , range 0.2 – 1.6‰ , $n = 3$), but more variable in membracids where four of six samples were ${}^{15}\text{N}$ depleted (-0.5 , -1.3 to 0.9‰ , $n = 6$). Inversely, Sternorrhyncha (coccoids from four families and aphids) were invariably enriched in ${}^{15}\text{N}$ compared to their hosts ($1.4 \pm 0.6\text{‰}$, 0.4 – 2.2‰ , $n = 9$), but more variable and mostly depleted in ${}^{13}\text{C}$ ($-1.1 \pm 1.8\text{‰}$, -4.1 to 1.9‰ , $n = 9$).

Ants

Isotope signatures of the 50 ant species (listed in Appendix) covered a broad range, encompassing 7.1‰ in $\delta^{15}\text{N}$ and 6.8‰ in $\delta^{13}\text{C}$, thus exceeding two typical transfers between trophic levels in N (3.4‰) (Fig. 1b).

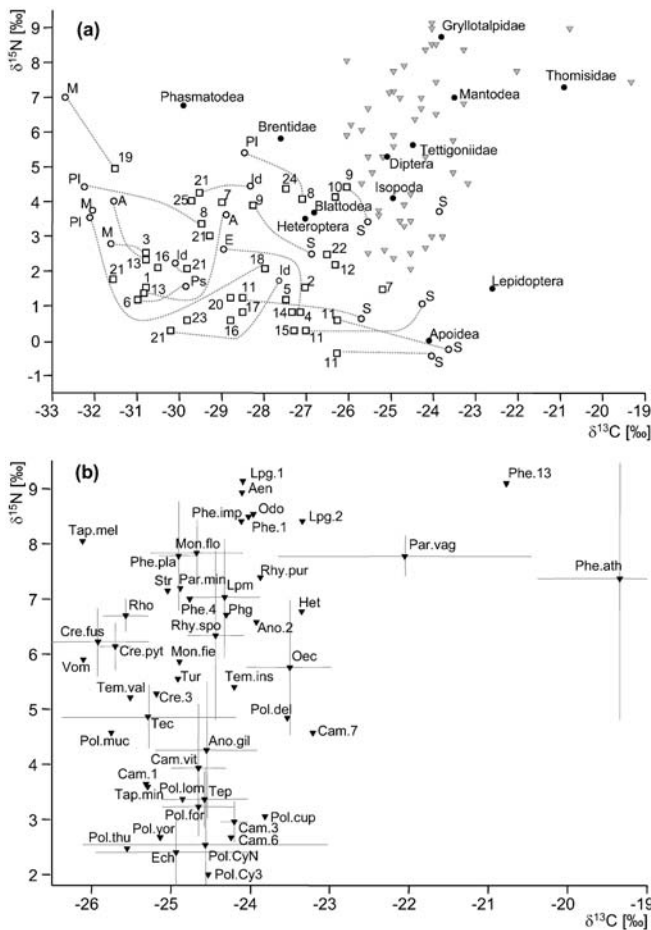


Fig. 1 Isotope composition ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of **a** plants, homopterans and other arthropods, and **b** ants from the study site. Plants are represented by \square (with number code, see Appendix), homopterans by \circ (with letter code, see Appendix), other arthropods by \bullet , and ants by ∇ , \blacktriangledown (**a**, **b**). Homopterans and their respective host plant are connected by a dotted line. Each ant species with multiple sampled colonies is represented by its mean and SD bars (for sample size and full species names, see Appendix)

Signatures of ants overlap with those of several arthropod orders that include typical predators or herbivores (Fig. 1a). No significant correlation was found between $\delta^{15}\text{N}$ of ants and $\delta^{15}\text{N}$ of plant individuals or species from which they were collected ($r=0.22$, $P=0.09$), while $\delta^{13}\text{C}$ signatures showed a weak positive correlation ($r=0.35$, $P<0.01$, both $n=59$ sample pairs).

On the community level omnivory of ants was confirmed by N but not C isotopes in a null model test proposed by Ponsard and Arditi (2000): the variance of $\delta^{15}\text{N}$ among all ant species ($\sigma_a^2=4.4\text{‰}$) was significantly larger than the expected variance of trophic transfers ($F_{49,25}=\sigma_a^2/\sigma_\Delta^2=3.6$, $P<0.001$), but not for $\delta^{13}\text{C}$ ($\sigma_a^2=1.5\text{‰}$, $F_{49,75}=0.8$, $P=0.87$).

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in ant species were significantly correlated ($r=0.31$, $P=0.03$, $n=50$). Isotopic signatures varied significantly between ant species and subfamilies. Both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ contributed significantly to the variation between species (ANOVA, $\delta^{15}\text{N}$, $F_{17,62}=10.2$,

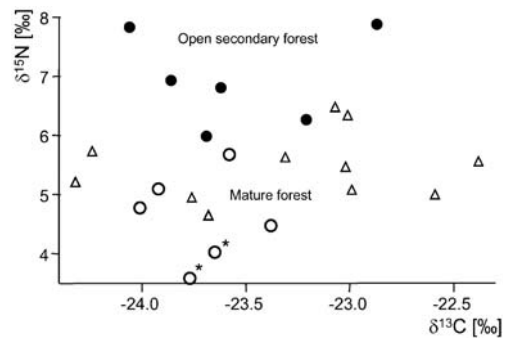


Fig. 2 Isotope signatures of 23 *Oecophylla smaragdina* colonies. Site-1 is represented by \triangle , site-2 by \bullet (naturally regenerating forest) or \circ (mature forest). * Indicates two colonies from a mature beach forest near site-2

$P<0.001$; $\delta^{13}\text{C}$, $F_{17,62}=15.9$, $P<0.001$). Interspecific variability was also significant when isotope values for plants from which each ant colony had been collected were included as covariate (ANCOVA, $\delta^{15}\text{N}$, $F_{15,34}=8.6$, $P<0.001$; $\delta^{13}\text{C}$, $F_{15,34}=11.4$, $P<0.001$). The four major ant subfamilies differed significantly only in $\delta^{15}\text{N}$ ($F_{3,44}=17.7$, $P<0.001$), but not in $\delta^{13}\text{C}$ ($F_{3,44}=0.8$, $P=0.51$). Isotope signatures of 23 *Oecophylla smaragdina* colonies are displayed in Fig. 2. No significant variation was found between *O. smaragdina* colonies from the two sites (MANOVA, $F_{2,20}=1.6$, $P=0.23$). However, there was a pronounced effect of successional forest stages: *O. smaragdina* colonies in recently reforested areas at site-2 had significantly lower $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ ($F_{1,21}=0.2$, $P=0.69$).

Ant larvae differed from adults in isotopic composition (species marked in Appendix). In six out of seven species tested, $\delta^{13}\text{C}$ 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 $\delta^{15}\text{N}$ (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 $\delta^{13}\text{C}$ and 0.1–0.6‰ in $\delta^{15}\text{N}$, 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 $\delta^{13}\text{C}$, but not for $\delta^{15}\text{N}$ (Wilcoxon matched pairs, $\delta^{13}\text{C}$, $Z=2.3$, $P=0.02$; $\delta^{15}\text{N}$, $Z=1.5$, $P=0.13$). Differences in isotope composition were also found between worker castes. There was a consistent trend in $\delta^{15}\text{N}$ across five species where samples included head and alitrunk (marked in Appendix): major workers had a significantly lower $\delta^{15}\text{N}$ than minors (reduced by 0.3–1.1‰, $Z=2.0$, $P=0.04$), while $\delta^{13}\text{C}$ did not vary significantly between castes ($Z=0.7$, $P=0.50$). This trend for $\delta^{15}\text{N}$ was not found in pupae that would have developed into major and minor workers (differences in $\delta^{15}\text{N}$ $<0.1\text{‰}$, $n=2$ 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 $\delta^{15}\text{N} < 0.2\text{‰}$, $n=2$).

C and N concentrations

Dry mass C and N concentrations (M_C and M_N , respectively) showed relatively little variation across workers of different ant species (mean \pm SD, M_C , 51.4 \pm 3.3%; M_N , 13.4 \pm 1.0%; C:N ratio, 3.8 \pm 0.4; $n=47$ species means). No significant correlation was found between M_N and $\delta^{15}\text{N}$ ($r=0.10$, $P=0.50$) or between the C:N ratio and $\delta^{15}\text{N}$ ($r=-0.07$, $P=0.65$). The same conclusions hold true when ant genera instead of species are used as units (M_N and $\delta^{15}\text{N}$, $r=0.18$, $P=0.40$; C:N and $\delta^{15}\text{N}$, $r=-0.15$, $P=0.48$, $n=24$). Furthermore, M_N showed only little and marginally significant variation between the four major ant subfamilies (mean \pm SD, Dolichoderinae, 13.5 \pm 0.4%, $n=7$ species means; Formicinae, 13.0 \pm 0.8%, $n=16$; Myrmicinae, 13.9 \pm 0.9%, $n=17$; Ponerinae, 13.0 \pm 1.6%, $n=6$; $F_{3,42}=2.5$, $P=0.07$). 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 (8.0 \pm 1.2%, $n=7$ species) and pupae (9.3 \pm 1.4%, $n=7$) than for adult workers of the same colony (paired t -tests, adults vs. larvae, $t=11.9$; adults vs. pupae, $t=8.6$, both $P<0.001$; see Appendix for selected species). Furthermore, the four homopteran taxa had significantly lower M_N than ant workers (10.1 \pm 2.6%; $F_{1,50}=31.8$, $P<0.001$) and significantly higher C:N ratios (6.2 \pm 3.2%; $F_{1,49}=28.3$, $P<0.001$).

Discussion

Trophic structure of the ant community

N isotope signatures of 50 Australian rainforest ant species indicate that ant communities represent a continuum from herbivores to predators, with pronounced omnivory. Parallel to our work, Davidson et al. (2003) analysed the N isotope composition of ant communities from rainforests in Peru and Borneo and came to similar conclusions. These findings 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 as judged by $\delta^{15}\text{N}$ signatures (*Camponotus*, *Echinopla*, *Polyrhachis*, *Tetraponera*).

These species were frequently observed at extrafloral and floral nectaries (Blüthgen 2003, see Appendix for general foraging observations), but not found to attend homopterans in the study site, although these four genera are generally known as trophobiotic elsewhere. In contrast, the dominant ants *Anonychomyrma gilberti* and *Oecophylla smaragdina* showed intermediate trophic positions. Both species had very large colonies and were highly territorial (Hölldobler 1983; Andersen 1995, own observations). They were the most abundant ants on honeydew and nectar sources particularly in the canopy of the study site, but also regularly observed preying on various arthropods (Blüthgen and Fiedler 2002, Floren et al. 2002, Blüthgen 2003). The distribution of these species seems to be particularly shaped by productive honeydew sources that are more predictable than prey (Blüthgen and Fiedler 2002, Blüthgen 2003). The subdominant understory ants (*Crematogaster*, *Paratrechina*, *Rhoptromyrmex*, *Technomyrmex*) showed even higher trophic positions, although regularly feeding on both honeydew and nectar (Blüthgen 2003). Despite the important contribution of plant-based diets to these ants' nutrition and distribution, 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). The highest levels of predation as indicated by $\delta^{15}\text{N}$ are found for ants that are most active in the understory or exclusively ground-foraging (see Appendix). 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 and Macauley 1981; Shattuck 1999), although they were repeatedly observed feeding from extrafloral nectaries or artificial sugar solutions. Correspondingly, the most common ponerine species on nectar sources (*Rhytidoponera spoliata*) had the lowest $\delta^{15}\text{N}$ values of this subfamily. Some *Pheidole* species and *Pheidologeton affinis* were predominantly ground-foraging, but besides predation and scavenging, occasional seed or fruit flesh consumption (Appendix; Briese and Macauley 1981) may play a certain role. Moreover, intraguild predation may be pronounced, since ant corpses provide large proportions of prey caught by *Oecophylla* (personal observation) or other ants (Briese and 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.

Do isotope signatures reflect trophic positions or substrate variability?

In the investigated ant community, $\delta^{15}\text{N}$ but not $\delta^{13}\text{C}$ correlated with predicted trophic positions; this was also found in a soil food web study (Ponsard and Arditì 2000).

Several lines of evidence suggest that variation of $\delta^{15}\text{N}$ among ants depicts real trophic positions rather than sheer plant substrate variability from which ants were collected:

1. There was no correlation between $\delta^{15}\text{N}$ of ants and plants, while plant-sucking homopterans and their hosts were strongly correlated. In contrast, $\delta^{13}\text{C}$ 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 of limiting the 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.

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 the C isotope composition of ants (Fisher et al. 1990; Rico-Gray and Sternberg 1991; Sagers et al. 2000). However, our results about N isotopes emphasize the important contribution of N from these plant-based resources (see also Fischer et al. 2002, Davidson et al. 2003). Further studies using controlled diets will be needed to evaluate the proportions of C and N flows from different sources and compounds, and differential effects of isotopic fractionation. Curiously, $\delta^{15}\text{N}$ of ants showed a greater overlap with that of plant foliage than did $\delta^{13}\text{C}$. Limited evidence from a few studies suggests that different plant products and tissues vary in isotope composition (Gleixner et al. 1993; Bauer et al. 2000; Schmidt and Stewart 2003), and such differences may be linked to the observed pattern. For example, plant leaf tissues may not equally well represent $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ of nectar or honeydew consumed by ants.

Intraspecific and ontogenetic variability

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 a similar isotope composition. In the

complex canopy of mature forests, these ants often attend large homopteran aggregations, particularly on two leguminous lianas (Blüthgen and Fiedler 2002). 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* (Blüthgen 2003). Thus, suitable honeydew and nectar sources in mature forests allow *Oecophylla* to include them as a 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 suggested by the isotope composition. This may explain the apparent discrepancies between observations and isotope results in those ant species that commonly attended homopterans in the understory (*Crematogaster*, *Paratrechina*, *Rhoptromyrmex*, *Technomyrmex*) and were among the most frequently occurring ants on nectaries as well. Isotope signatures of larvae and pupae from ten species were indeed very similar to those of adults in our study. Only a slight increase in $\delta^{15}\text{N}$ (and sometimes $\delta^{13}\text{C}$) was found that might be explained by the direct contribution of the stomach contents in larvae (empty in pupae and removed from adults), or by ageing [see Ponsard and 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).

Tissue N concentration

Davidson and Patrell-Kim (1996) proposed that canopy ants which live on N-poor plant exudates may have developed mechanisms to reduce N requirements, e.g. through a thinner exoskeleton. They suggested that herbivorous ants might have reduced N concentrations and found some support for this idea in a preliminary analysis of 11 ant species in Panama. However, in our

study C and N 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 N to a great extent. "Classic" herbivores such as homopterans showed much lower N concentrations. Other strategies proposed by Davidson (1997) include N-poor chemical defence or "high tempo" activity, and may explain better the ants' success in the canopy habitats.

Plants and homopterans

Plant samples from our study site showed low overall ^{15}N abundance (see Högberg 1997) and no indication of CAM or C_4 metabolism (see Winter et al. 1983). The observed level and variability of plant $\delta^{13}\text{C}$ in Australia is typical for C_3 plants in other rainforests (Guehl et al. 1998; Bonal et al. 2000; Nagy and Proctor 2000). C_4 or CAM may be more prominent in other habitats and life forms such as epiphytes, but 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 and Stewart 2003), variation between homopterans and leaf samples may thus be linked to these variable feeding modes of homopterans. Besides substrate effects, the digestive microflora 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.

Conclusions

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. N 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 understory or canopy plants, while predation is most pronounced in ground-foraging species. *O. smaragdina* and all subdominant understory 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 C for adult metabolism, but also serve as an important source of N for larval growth.

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Appendix

For ant, plant and homopteran species and their codes used in Fig. 1 see Table 1

Table 1 Ant, plant and homopteran species and their codes used in Fig. 1. Sample sizes (n) are number of ant or homopteran colonies or plant individuals analysed. *P* Observed foraging on plant foliage,

N observed feeding on nectar, *H* observed feeding on honeydew, *F* observed feeding on fruit flesh, *S* observed feeding on sugar solutions, *G* only observed on the ground or lower tree trunks

Code	(Sub)family	Species	Foraging observations	n
Ants (Hymenoptera: Formicidae)				
Aen	Aenictinae	<i>Aenictus aratus</i> Forel	G	1
Ano.gil	Dolichoderinae	<i>Anonychomyrma gilberti</i> (Forel)	P, N, H, S	9
Ano.2		<i>A. sp. 2</i>	P, N	1
Lpm		<i>Leptomyrmex unicolor</i> Emery	P, N, F, S	3
Tap.mel		<i>Tapinoma melanocephalum</i> (Fabricius) ^a	P, N, S	1
Tap.min		<i>T. minutum</i> Mayr	P, N, S	1

Table 1 (continued)

Code	(Sub)family	Species	Foraging observations	<i>n</i>
Tec		<i>Technomyrmex albipes</i> (Smith) ^{a, b}	P, N, H, S	3
Tur		<i>Turneria bidentata</i> Forel ^a	P, N	1
Cam.1	Formicinae	<i>Camponotus</i> sp. 1 (<i>macrocephalus</i> gp.)	P, N, S	1
Cam.3		<i>C.</i> sp. 3 (<i>novae-hollandiae</i> gp.) ^c	P, N, S	3
Cam.6		<i>C.</i> sp. 6 (<i>gasseri</i> gp.)	P, N, S	1
Cam.7		<i>C.</i> sp. 7 (<i>extensus</i> gp.) ^d	P, S	1
Cam.vit		<i>C. vitreus</i> (Smith) ^{a, b, d, e}	P, N, S	3
Ech		<i>Echinopla australis</i> Forel ^{a, b}	P, N, S	3
Oec		<i>Oecophylla smaragdina</i> (Fabricius) ^{a, b, c, d, e}	P, N, H, S	23
Par.min		<i>Paratrechina minutula</i> (Forel)	P, N, S	1
Par.vag		<i>P. vaga</i> (Forel) ^a	P, N, H, F, S	3
Pol.Cy3		<i>Polyrhachis</i> (<i>Cyrtomyrma</i>) "Cyrto 03" Kohout	P, N	1
Pol.CyN		<i>P.</i> (<i>Cyrtomyrma</i>) "Cyrto NB5041" Kohout ^c	P, N, S	3
Pol.yor		<i>P.</i> (<i>Cyrtomyrma</i>) <i>yorkana</i> Forel	P, N, F, S	2
Pol.thu		<i>P.</i> (<i>Hagiomyrma</i>) <i>thusnelda</i> Forel	P, N	1
Pol.cup		<i>P.</i> (<i>Hedomyrma</i>) <i>cupreata</i> Emery	P, N, S	1
Pol.for		<i>P.</i> (<i>Myrma</i>) <i>foreli</i> Kohout	P, N, S	3
Pol.lom		<i>P.</i> (<i>Myrmatopa</i>) <i>lombokensis</i> Emery	P	1
Pol.muc		<i>P.</i> (<i>Myrmhopla</i>) <i>mucronata</i> Smith	P, N, S	1
Pol.del		<i>P.</i> (<i>Myrmothrinax</i>) <i>delicata</i> Crawley	P, N, S	1
Cre.fus	Myrmicinae	<i>Crematogaster</i> cf. <i>fusca</i> Smith	P, N, H, S	3
Cre.pyt		<i>C.</i> cf. <i>pythia</i> Forel ^b	P, N, S	3
Cre.3		<i>C.</i> sp. 3	P, N, S	1
Mon.fie		<i>Monomorium fieldi</i> var. <i>laeve-nigrius</i> Forel	P, N, S	1
Mon.flo		<i>M. floricola</i> Forel ^b	P, N, S	3
Phe.imp		<i>Pheidole impressiceps</i> Mayr	P, N, F, S	1
Phe.pla		<i>P. platypus</i> Crawley ^d	P, N, F, S	3
Phe.1		<i>P.</i> sp. 1	P, N, F, S	1
Phe.4		<i>P.</i> sp. 4	G, F	1
Phe.13		<i>P.</i> sp. 13	P, H	1
Phe.ath		<i>P.</i> cf. <i>athertonensis</i> Forel ^{b, d}	P, N, F, S	3
Phg		<i>Pheidologeton affinis</i> (Jerdon)	G, F, S	1
Rho		<i>Rhoptromyrmex wroughtonii</i> Forel	P, N, H, S	3
Str		<i>Strumigenys guttulata</i> Forel	P, N	1
Tem.ins		<i>Tetramorium insolens</i> (F. Smith)	P, N, S	1
Tem.val		<i>T. validiusculum</i> Emery	P, N, S	1
Vom		<i>Vombisidris australis</i> (Wheeler)	P	1
Het	Ponerinae	<i>Heteroponera</i> sp. 1	P, S	1
Lpg.1		<i>Leptogenys</i> sp. 1	G	1
Lpg.2		<i>L.</i> sp. 2	G	1
Odo		<i>Odontomachus ruficeps</i> Smith	P, N, F, S	1
Rhy.pur		<i>Rhytidoponera purpurea</i> (Emery)	P, S	1
Rhy.spo		<i>R. spoliata</i> (Emery)	P, N, S	3
Tep	Pseudomyrmecinae	<i>Tetraponera nitida</i> (Smith)	P, N, S	3
"Homoptera" (Hemiptera: Sternorrhyncha and Auchenorrhyncha)				
A	Aphidae	<i>Aphis clerodendri</i> Matsumura		2
Id	Cicadellidae	Idiocerinae: Gen. nov.		3
M	Coccidae	<i>Milviscutulus mangiferae</i> (Green)		3
Ps	Diaspididae	<i>Pseudaulacaspis</i> sp.		1
E	Eriococcidae	(Genus not identified)		1
S	Membracidae	<i>Sextius "kurandae"</i>		7
Pl	Pseudococcidae	<i>Planococcus minor</i> (Maskell)		3
Plants				
1	Areaceae	<i>Licuala ramsayi</i> (F. Muell) Domin		1
2		<i>Normanbya normanbyi</i> (W.Hill) L. H. Bailey		1
3	Asclepiadaceae	<i>Melodinus australis</i> Pierre		1
4	Convolvulaceae	<i>Merremia peltata</i> Merr.		1
5	Eleocarpaceae	<i>Elaeocarpus angustifolius</i> Blume		1
6	Euphorbiaceae	<i>Aleurites rockinghamensis</i> (Baill.) P. I. Forster		1
7		<i>Macaranga involucrata mallotoides</i> (F. Muell.) L. M. Perry		2
8		<i>M. tanarius</i> Muell. Arg.		2
9	Fabaceae s.l.	<i>Caesalpinia traceyi</i> L. Pedley		2
10		<i>Castanospermum australe</i> A. Cunn. & C. Fraser ex Hook.		1
11		<i>Entada phaseoloides</i> Merr.		4
12	Flagellariaceae	<i>Flagellaria indica</i> L.		1
13	Lamiaceae	<i>Clerodendrum tracyanum</i> (F. Muell.) Benth.		1

Table 1 (continued)

Code	(Sub)family	Species	Foraging observations	<i>n</i>
14	Lauraceae	<i>Cryptocarya hypospodia</i> F. Muell.		1
15		<i>C. murrayi</i> F. Muell.		1
16		<i>Endiandra microneura</i> C. T. White		2
17	Meliaceae	<i>Dysoxylum pettigrewianum</i> F. M. Bailey		1
18	Moraceae	<i>Ficus destruens</i> C. T. White		1
19	Myrsinaceae	<i>Ardisia pachyrrhachis</i> (F. Muell.) F. M. Bailey		1
20	Myrtaceae	<i>Acmena graveolens</i> L. S. Smith		1
21		<i>Syzygium erythrocalyx</i> B. Hyland		5
22		<i>S. gustavioides</i> (F. M. Bailey) B. Hyland		1
23		<i>S. sayeri</i> (F. Muell.) B. Hyland		1
24	Proteaceae	<i>Cardwellia sublimis</i> F. Muell.		1
25	Sterculiaceae	<i>Argyrodendron peralatum</i> (Bailey) Edlin ex J. H. Boas		1

^a Additional sampling of larvae

^b Additional sampling of pupae

^c Additional sampling of minor and major caste separately: worker head only

^d Additional sampling of minor and major caste separately: worker head and alitrunk

^e Additional sampling of minor and major caste separately: pupae

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