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Trophic ecology of tropical leaf litter ants (Hymenoptera: Formicidae) – a stable isotope study in four types of Bornean rain forest*

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Abstract

We measured δ ^{15}N values and inferred the trophic positions of 151 ground ant species from four types of rain forests (alluvial, limestone, dipterocarp forest, and Kerangas) in Gunung Mulu National Park, in Sarawak, Malaysia. Four hypotheses were tested: 1) Ground-foraging ants occur in all trophic levels; 2) ant subfamilies differ in their trophic status; 3) δ ^{15}N values differ among species within genera and among genera within subfamilies; and 4) ant assemblages in different forest types differ in their trophic structure. Base-line corrected mean δ ^{15}N values for different ant species ranged from -0.67‰ to 10.56‰ thus confirming that forest ants occupy a variety of trophic levels. Based on stable isotopes we distinguished three major trophic groups: a) species mostly feeding on hemipteran exudates and other plant-derived food resources; b) omnivorous species with mixed diet of plant and animal prey; and c) truly predacious species, including arthropod specialists. Ant subfamilies differed significantly in their trophic positions, as did many ant genera within subfamilies and ant species within ant genera. Several ant species exhibited dietary flexibility and differed significantly in trophic positions across forest types.

Key words: Trophic position, stable isotopes, food webs, functional groups, leaf litter ants.

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Introduction

Stable isotope analysis as a method for studying ants. Ants exhibit a wide variety of feeding habits and are able to occupy almost all trophic levels in a food web (HÖLLDOBLER & WILSON 1990). The analysis of stable isotopes is a standard method for uncovering trophic relationships in ecological research (TILLBERG & al. 2006, FIEDLER & al. 2007, OTTONETTI & al. 2008, FELDHAAR & al. 2010). This method is based on the discrimination of lighter and heavier non-radioactive isotopes during metabolic processes, which result in an enrichment of the heavier isotopes in the food chain, thus making the energy flow through the system detectable (SULZMAN 2008). In contrast to direct feeding observations, which give an exact snapshot of the diet at the moment of observation with detailed information on the consumed food, the evaluation of stable isotopes can provide information on long-term dietary sources that is otherwise difficult to obtain. It is therefore a method especially suited for a species-rich and sometimes inconspicuous animal group such as ants (FIEDLER & al. 2007). Isotopic enrichment from one trophic level to another was measured experimentally for the ant species *Camponotus floridanus* by FELDHAAR & al. (2010). Based on their findings, 3.0‰ enrichment of ^{15}N for each trophic level is considered a general rule in studies on ants (BLÜTHGEN & FELDHAAR 2009).

Stable isotope studies have explored various aspects of myrmecology, including studies of agricultural ecosystems (OTTONETTI & al. 2008), trophic relations of invasive and native ant species (LEBRUN & al. 2007, TILLBERG & al. 2007), special trophic relationships between ants and other organisms (CLEMENT & al. 2008), and comparisons between the nutrition and ecology of parabiotic ant species (MENZEL & al. 2012).

Few studies have investigated the trophic structure of tropical ant communities. BIHN & al. (2010) included trophic positions in a functional diversity approach on neotropical ant communities and WOODCOOK & al. (2012) used Bornean ant communities in a methodological stable isotope study. Neither of these papers, however, presented details on trophic positions of single species. HYODO & al. (2011) studied the feeding habits of Hymenoptera and Isoptera in Sarawakian rainforest (Malaysia), but included only two leaf litter ant species.

Studies of tropical ant communities using stable isotope analysis are scarce. DAVIDSON & al. (2003) compared a Neotropical with an Oriental ant community and BLÜTH-

* This paper is dedicated to the memory of late Prof. Dr. Elisabeth Kalko in honour of her outstanding contribution as researcher and mentor.

GEN & al. (2003) studied an Australian ant community. Both studies focused on arboreal species that have a strong trophic relationship with hemipterans and regularly use extrafloral nectaries (EFNs) as sources of energy. By use of stable isotopes the authors demonstrated that most tropical arboreal ant species are herbivores, which feed on abundant canopy resources of honeydew and EFNs (TOBIN 1994). Ground living ant species were covered in these studies only to provide a general comparison with arboreal species and were all categorised as predators.

Bornean ground ant feeding habits. In the Oriental region, Borneo has especially high ant species richness, with 717 valid species and 52 additional subspecies from 12 subfamilies (PFEIFFER & al. 2011). High diversity has been reported for both arboreal (FLOREN & LINSENMAIR 2005) and leaf litter ants (MALSCH & al. 2008, PFEIFFER & MEZGER 2012). Bornean ants exhibit a wide variety of feeding habits (Figs. 1 - 4) which make them the most important invertebrate predators in soil and leaf litter, having a considerable influence on arthropod communities (BERGHOFF & al. 2003). The level of prey specialisation varies among different ground-foraging ant species. Genera like *Strumigenys* or other Dacetini contain species that specialise on collembolans, diplurans, mites, termites, and other soil invertebrates (BOLTON 2000), while *Aenictus* and *Cerapachys* prey on other ants (HÖLLDOBLER 1982, HIROSAWA & al. 2000). Species in other genera such as *Diacamma* are generalist predators (MALSCH & al. 2008). Otherwise many ant species are considered as omnivores or as scavengers. *Pheidole* species are major seed collectors, but also exhibit predatory behaviour (PFEIFFER & al. 2006). A few species are adapted to use fungi as a food resource, as in certain *Euprenolepis* species (WITTE & MASCHWITZ 2008). Many ant species are, however, directly or indirectly reliant on plants, as EFNs and sugar-containing exudates of hemipterans are their major food sources (BLÜTHGEN & al. 2006, PFEIFFER & LINSENMAIR 2007). Although most such species are arboreal, some ground living species are also adapted to this feeding habit, e.g., several *Pseudolasius* species keep subterranean mealy-bugs as trophobionts (MALSCH & al. 2001).

Study purpose and aim. There is a paucity of knowledge on the trophic structure of tropical soil- and leaf-litter ant communities and the trophic positions of species in ground food webs. Our research is aimed at studying whether non-arboreal ant taxa are in really mostly predatory (see BLÜTHGEN & al. 2003) or if phylogenetic relationships play a role in determining trophic status.

We conducted our research on specimens collected during a previous project that compared different types of primary rain forest in Sarawak, Malaysia, in order to explore the impact of environmental variation on ground ant diversity (MEZGER & PFEIFFER 2010c, 2011). Our research area in Gunung Mulu National Park comprised four types of tropical lowland forest, each with differing soil types, plant cover and flooding regime (see Methods): alluvial forest, limestone forest, dipterocarp forest and kerangas. We found high beta diversity between forest types (PFEIFFER & MEZGER 2012), thus corroborating the impact of habitat heterogeneity on these extra-diverse ground ant communites, with 206 species altogether.

Using isotope data of the most common 151 ant species, we tested the following hypotheses: 1) Ground-foraging ants occur in all trophic levels; 2) ant subfamilies differ in their trophic status; 3) $\delta^{15}N$ values differ among species within genera and among genera within subfamilies; and 4) ant assemblages in different forest types differ in their trophic structure.

Material and methods

Study site. The study was conducted in Gunung Mulu National Park (Mulu NP) (4° 57' N, 114° 47' E) in Sarawak (Malaysia) on Borneo (HAZEBROEK & MORSHIDI 2001), in a highly diverse area previously explored by the 1977 / 78 Borneo expedition of the Royal Geographical Society (JERMY 1982). The climate in the lowlands of this 528 km^2 area is tropical wet with mean air temperatures of about 26°C and 4000 to 5000 mm rainfall per year (Sarawak Weather Service, pers. comm.). All field work was conducted from 1st April 2006 to 17th October 2007. Sampling was performed in four types of primary lowland forest in large, continuous forest tracts, each with a size of at least several square kilometers (HAZEBROEK & MORSHIDI 2001). The different habitats are described as follows; further details on the habitats are presented in Table 1 and in MEZGER & PFEIFFER (2011).

1) Alluvial forests are frequently inundated by water. The lower, more flood-prone tracts grow on gley soils from the Bijat-family, whereas the higher areas grow on podzolic or peaty soils with shallow top-soil (PROCTOR & al. 1983, MEZGER & PFEIFFER 2011). Alluvial forests in Mulu NP are rich in tree species and dominated by Leguminosae and to a lesser extent by Ebenaceae, Euphorbiaceae, and Dipterocarpaceae trees (PROCTOR & al. 1982).

2) Limestone forests are found on steep terrain. Their shallow soils consist largely of mull humus (0 - 50 cm in depth), which is irregularly interrupted by jagged limestone rocks. In terms of flora, these forests are relatively species-poor and dominated by trees of the Dipterocarpaceae (PROCTOR & al. 1983).

3) Lowland mixed dipterocarp forest grows on red-yellow podzolic soils with a substantial organic layer of up to 15 cm (MEZGER & PFEIFFER 2011). This type of forest is floristically species-rich and trees of the dominant family, the Dipterocarpaceae, reach heights of up to 57 metres (PROCTOR & al. 1983).

4) Kerangas or heath forests rise on terraces with sandy organic podzols, which are sometimes waterlogged and anaerobic; these forests are of intermediate tree species-richness and dominated by Dipterocarpaceae, Guttiferaceae and Myrtaceae (PROCTOR & al. 1982).

Sample design. During a study on community ecology of soil and leaf litter ants (MEZGER & PFEIFFER 2010a, 2010b, 2010c, 2011, PFEIFFER & MEZGER 2012) we collected 100 Winkler samples according to the ALL-protocol (AGOSTI & ALONSO 2000). In each forest type we established 20 sample plots along a 400 m transect. In alluvial forest and limestone forest we collected ten further samples at distinct 200 m transects that were several kilometers apart. A map with sampling localities is given in MEZGER & PFEIFFER (2011).

This method proved to be effective as it reached a sample coverage (the percentage of sampled species from the estimated species) of 79% for the whole forest and between 60 to 72% for the single forest types (PFEIFFER & MEZGER 2012). A high percentage of the species found in

Figs. 1 - 4: (1) Foragers of *Myrmicaria* sp. gathering honeydew from a Membracidae hopper in the lower vegetation; (2) workers of *Pheidologeton affinis* collecting a seed; (3) a squad of *Leptogenys* sp. 6 transporting a captured Platyrhacidae centipede; (4) opportunistic foragers of *Dolichoderus indrapurensis* gather around a valuable food resource.

Tab. 1: Ecological parameters for the four forest types, including their SD in parenthesis where appropriate, based on unpublished data and MEZGER & PFEIFFER (2010). Details on the measurement of vegetation cover provided in MEZGER & PFEIFFER (2010). Data includes altitude above sea level, soil depth, vegetation cover, number of ant species, sample coverage including estimator and individual numbers of arthropods according to PFEIFFER & MEZGER (2012).

Forest type	**Alluvial forest**	**Limestone forest**	**Dipterocarp forest**	**Kerangas**
Altitude a.s.l.	50 - 60 m	75 - 250 m	200 - 300 m	180 - 200 m
Mean soil depth	4.2 cm (± 1.1) [n = 30]	5.3 cm (± 2.3) [n = 30]	6.1 cm (± 2.8) [n = 20]	8.3 cm (± 2.5) [n = 20]
Mean vegetation cover	17.2 points / m² (± 13.5) [n = 30]	13.5 points / m² (± 7.3) [n = 30]	6.2 points / m² (± 4.8) [n = 20]	5.7 points / m² (± 10.0) [n = 20]
Total number of ant species	110 [n = 30]	130 [n = 30]	89 [n = 20]	69 [n = 20]
Sample coverage (Estimator)	72.4% (Jackknife 1)	61.6% (Jackknife 2)	63.5% (Jackknife 2)	59.7% (Jackknife 2)
Mean no. of arthropods per m²	876 (± 700) [n = 24]	857 (± 565) [n = 25]	569 (± 363) [n = 17]	316 (± 183) [n = 17]

each forest type by Winkler samples is evaluated in the present study (alluvial forest: 81%, limestone forest: 46%, dipterocarp forest: 70% and Kerangas: 59%). 107 of the 151 studied ant species were caught by Winkler traps.

We used several other collecting methods, such as Barber traps (filled with salty water and detergent and opened 48 hours), bait stations, sweep netting, yellow pans, and opportunistic sampling to enhance our sample size of ants and other arthropod species, especially herbivores (Curculionidae, Lepidoptera, and Orthoptera) and other carnivorous arthropods (Staphylinidae, Carabidae, Reduviidae, and Araneida), which were taken as references for different trophic levels (TILLBERG & al. 2007). Further ant species were hand-caught after behavioural observations (Figs. 1 - 4) to ensure that all abundant species of the habitat were represented in our collection.

As short-term storage in ethanol has no effect on isotope ratio (FELDHAAR & al. 2010), collected organisms were killed in ethanol before they were dried at 30°C for 48 hours with a desiccation machine (Stöckli, Dörrex, 600W). Samples were then preserved in dry NaCl, as recommended by S. Ponsard (pers. comm.) and tested in trials. In this manner 358 samples of ants were collected. Additionally we prepared 98 specimens that had been stored in ethanol for a longer period; long term storage may produce a shift in $\delta^{13}C$, but not in $\delta^{15}N$ values (TILLBERG & al. 2006). We further collected samples of leaf litter, topsoil and subsoil (in 10 cm depth) of all four forest types at the sample plots of our study.

Identification of ant genera was performed by reference to BOLTON (1994) with details on species identification being published elsewhere (PFEIFFER & al. 2011). We kept voucher specimens of all ant species used in the study, for identification. These are deposited at the "AntBase.Net collection" of the University of Ulm (ABNC), currently housed at the University of Landau, Germany, with Automontage© photographs of most species available via http://www.antbase.net.

Isotopic analyses. According to the size of the respective ant species, we used one to five specimens in one sample. For analysis of stable isotopes, we removed the ants' abdomina to avoid contamination of the samples by undigested food (BLÜTHGEN & al. 2003), but left the animals otherwise intact to avoid the loss of distinct fractions (e.g., lipids) during milling. For arthropod samples we used between 0.1 to 2.0 mg of tissue, while from the soil samples we used samples with weights from 2.5 to 5 mg, depending on their suspected nitrogen content. Stable isotope values were measured by isotope ratio mass spectrometry (Delta +, Thermo Finnigan) coupled to an elemental analyser (NA1110, CE – Instruments). Analyses were performed at the Centre for Stable Isotope Research and Analysis, University of Göttingen.

Statistical analysis. In order to compare ants from four different forest types, we needed a base-line of the $\delta^{15}N$ values in respective habitats, as different soil types differ in $\delta^{15}N$ content (SCHEU & FALCA 2000). As demonstrated by WOODCOCK & al. (2012) small scale base-line correction is necessary for an effective calibration. We corrected $\delta^{15}N$ values of samples for each transect separately. This ensured that all samples were taken within 500 m of a base-line sample (see WOODCOCK & al. 2012). For this purpose, we first calculated the means of all $\delta^{15}N$ values of topsoil and leaf litter from a given transect (Appendix S1, as digital supplementary material to this article, at the journal's web pages). The habitat value for a transect was then calculated as

$$\delta^{15}N_{habitat} = (\text{mean } \delta^{15}N_{leaf\ litter} + \text{mean } \delta^{15}N_{top\ soil}) / 2.$$

Because most samples (approximately 35%) were collected from the main transect in alluvial forest and this transect had the highest $\delta^{15}N_{habitat}$ value, we designated the habitat value from that transect as base-line and calculated the corrected $\delta^{15}N$ values for all samples according to this formula:

$$\delta^{15}N_{corrected} = \delta^{15}N_{measured} + (\delta^{15}N_{alluvial\ transect1} - \delta^{15}N_{habitat\ x}).$$

Therefore a correction value ($\delta^{15}N_{alluvial\ transect1} - \delta^{15}N_{habitat\ x}$) had to be added to each of the measured $\delta^{15}N$ values to allow comparison of habitats. These correction values were: 0 (alluvial forest transect 1), 0.55 (alluvial forest transect 2), 2.65 (limestone forest transect 1), 2.03 (limestone forest transect 2), 1.45 (dipterocarp forest) and 2.4 (Kerangas). Base-line corrected $\delta^{15}N$ values are henceforth referred to as "$\delta^{15}N_{cor}$".

Based on the findings of FELDHAAR & al. (2010), who studied *Camponotus floridanus* ants and reported an enrichment in $\delta^{15}N$ by 3.0‰ at each trophic level, we used a similar value to assess the number of trophic levels in a food web in the single forest types. We compared isotope signatures of all members of a trophic group with those of the arthropods we had sampled to check that our base-line calibration was valid.

To compare the length of the food chain between the four forest types, we compared the total range of isotope values as well as the range between the species with the lowest nitrogen isotope value (*Camponotus gigas*) and the highest nitrogen isotope value (*Mystrium camillae*) found in all forest types (C-M distance). During this analysis we corrected for $\delta^{15}N_{habitat}$ in those two forest types that comprised two transects: alluvial forest and limestone forest. Additionally, we used an F-test (R 2.11.1, stat package) to assess the differences in the distribution of the uncorrected $\delta^{15}N$ values among single transects.

To test our hypotheses that a species that occurs in several forest types may differ in its trophic status among these types, we tested all of those species that were collected three or more times in two or more forest types after having corrected for the respective base-line.

Results

Leaf litter and soil. We studied four types of forest with different soil types. The grand mean $\delta^{15}N$ values (leaf litter and topsoil combined) of these forests ranged from -0.52‰ in the Kerangas to 1.55‰ in the alluvial forest, with -0.44‰ in limestone forest and 0.43‰ in dipterocarp forest (Appendix S1). Each layer differed significantly between the four forest types (Kruskal Wallis ANOVAs: leaf litter $H_{(3, 45)} = 15.6$, top-soil $H_{(3, 49)} = 18.12$, P for all < 0.01, post hoc multiple comparisons). In all forest types $\delta^{15}N$ values increased with increasing soil depths, leaf litter layer had lower values than top-soil, and highest values were found in the sub-soil. These differences were significant in all forest types (KW ANOVAs: alluvial forest: $H_{(2, 40)} = 30.17$, $P < 0.001$; limestone forest: $H_{(1, 21)} = 8.14$, $P < 0.005$; Kerangas: $H_{(2, 21)} = 20.40$, $P < 0.001$; dipterocarp forest $H_{(2, 27)} = 32.69$, $P < 0.001$ post hoc multiple comparisons).

From all forest types we sampled herbivore (n = 31) and carnivore (n = 58) arthropod species as references (Appendix S2). In all forest types, the isotope values (non-corrected values) of both groups differed significantly (t-tests, alluvial forest $n_{herb} = 8$; $n_{car} = 25$; $t = -9.39$; $p < 0.001$; limestone forest $n_{herb} = 9$; $n_{car} = 12$; $t = -4.48$; $p < 0.001$; dipterocarp forest $n_{herb} = 7$; $n_{car} = 8$; $t = -4.31$; $p < 0.001$; Kerangas $n_{herb} = 7$; $n_{car} = 13$; $t = -4.43$; $p < 0.001$).

Trophic status of ants. We collected 500 samples of ants comprising 151 species. The mean $\delta^{15}N_{cor}$ values (base-line corrected) of the studied ants ranged from -0.67‰ (*Myrmicaria lutea*) to 10.56‰ (*Pheidologeton affinis*); a full list with the mean isotope values of all studied species is given in Appendix S3.

The $\delta^{15}N_{cor}$ values of the nine tested subfamilies (Formicinae, Dolichoderinae, Aenictinae, Myrmicinae, Pone-

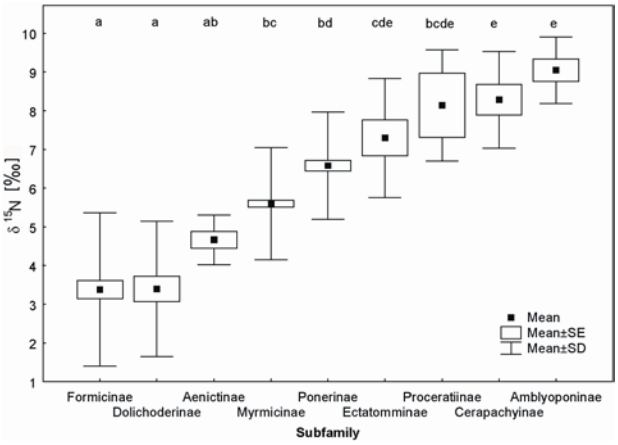


Fig. 5: δ ^{15}N values (base-line corrected) of nine subfamilies of ants differ significantly among each other. Different letters mark significant differences (ANOVA, post hoc HSD for unequal N). Sample size (i = number of species analysed, n = number of samples analysed) Formicinae: i = 13, n = 74; Dolichoderinae: i = 3, n = 28; Aenictinae: i = 3, n = 9; Myrmicinae: i = 41, n = 251; Ponerinae: i = 24, n = 105; Ectatomminae: i = 2, n = 11; Proceratiinae: i = 2, n = 3; Cerapachinae: i = 2, n = 10; Ambyoponinae: i = 2, n = 8.

Tab. 2: ANOVA results for a breakdown of δ ^{15}N values of ant genera within different ant subfamilies. Information presented includes respective subfamily, the number of tested ant genera, the degrees of freedom, F-values and p-values of the ANOVA and the number of pairs of genera with significant results in an Unequal N HSD post hoc test. * marks significant ANOVA value.

Subfamily	Tested genera	df	F value	p-value	Significant post-hoc results
Formicinae	7	6, 59	18.41	*< 0.00001	9
Dolichoderinae	4	3, 24	45.79	*< 0.00001	5
Myrmicinae	20	19, 228	5.74	*< 0.00001	10
Ponerinae	9	8, 96	4.35	*0.000167	2
Amblyoponinae	2	1, 7	17.35	*0.004216	1

rinae, Ectatomminae, Proceratiinae, Cerapachyinae, and Amblyoponinae) differed significantly among each other (ANOVA, $F_{(8, 488)}$ = 44.719, p = 0.0000; post hoc tests, Fig. 5).

When we tested whether ant genera differed in their corrected δ ^{15}N values within their subfamilies (ANOVA with Unequal N HSD post hoc test), we found significant differences in all of the five tested subfamilies and within altogether 28 pairs of genera (for ANOVA statistics see Table 2, for all mean δ $^{15}N_{cor}$ values, n and S.Ds., as well as the post hoc results see Appendix S4). The two Amblyoponinae genera tested, *Mystrium* (δ $^{15}N_{cor}$ = 9.29) and *Myopopone* (δ $^{15}N_{cor}$ = 7.11), differed significantly in δ $^{15}N_{cor}$ 15 values (p = 0.017). Within the Dolichoderinae *Dolichoderus* (δ $^{15}N_{cor}$ = 1.23), *Technomymrex* (δ $^{15}N_{cor}$ = 3.33) and *Philidris* (δ $^{15}N_{cor}$ = 5.88) differed among each other and all but *Philidris* also differed significantly from *Tapinoma* (δ $^{15}N_{cor}$ = 7.57). In the Ponerinae *Pachycondyla* (δ $^{15}N_{cor}$ = 7.47) differed from *Odontomachus* (δ $^{15}N_{cor}$ =

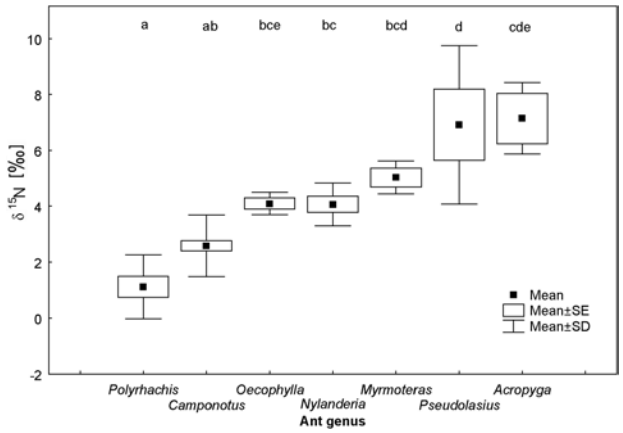


Fig. 6: Distribution of δ ^{15}N values in ant genera of the Formicinae. Given are the means for *Polyrhachis* (n = 9), *Camponotus* (n = 36), *Oecophylla* (n = 4), *Nylanderia* (n = 7), *Myrmoteras* (n = 3), *Pseudolasius* (n = 5), and *Acropyga* (n = 2). Similar letters indicate not significant differences in an unequal N HSD post hoc test after ANOVA (see Tab. 2).

Tab. 3: ANOVA results for a breakdown of δ ^{15}N values of ant species within different ant genera. Information presented includes the respective genus, the number of tested ant species, the degrees of freedom, F-values and p-values of the ANOVA, and the number of pairs of species with significant results in an Unequal N HSD post hoc test (see text). * marks significant ANOVA value.

Genus	Tested species	df	F value	p-value	Significant post-hoc results
Camponotus	3	2, 31	8.79	*0.00095	2
Crematogaster	3	2, 18	5.45	*0.01414	1
Hypoponera	4	3, 23	0.45	0.71928	0
Leptogenys	3	2, 7	9.10	*0.01131	1
Oligomyrmex	3	2, 10	18.15	*0.00047	3
Pheidole	9	8, 43	3.29	*0.00511	1
Strumigenys	4	3, 16	9.93	*0.00062	2

5.79, p = 0.017) and *Diacamma* (δ $^{15}N_{cor}$ = 5.65, p = 0.017). In the subfamily Myrmicinae we recorded significant differences between ten pairs of genera (see Appendix S4), and in Formicinae nine pairs of genera differed among each other (Fig. 6).

We used ANOVA to further test for differences of corrected δ ^{15}N values within species of the same genera and found significant differences for all of seven ant genera for which we had sufficient data, except *Hypoponera* (Tab. 3). In Unequal N HSD post hoc tests of the 29 involved species, ten pairs of species differed significantly from each other in their δ $^{15}N_{cor}$ values: e.g., in *Camponotus*, *C. saundersi* (δ $^{15}N_{cor}$ = 1.51) differed from *C. gigas* (δ $^{15}N_{cor}$ = 2.89, p = 0.014) and *C. arrogans* (δ $^{15}N_{cor}$ = 3.21, p = 0.002), in *Crematogaster*, *C. modiglianii* (δ $^{15}N_{cor}$ = 3.36) differed significantly from *C.* sp. 1 (δ $^{15}N_{cor}$ = 5.83, p = 0.01) and almost significantly from *C.* sp. 9 (δ $^{15}N_{cor}$ = 5.32, p = 0.058). *Leptogenys* sp. 1 (δ $^{15}N_{cor}$ = 6.86) differed from

Tab. 4: Comparison of $\delta^{15}N$ values for species collected in several forest types. For these analyses we used all species which were collected in two or more forest types with at least three replicates in each type. We show species name, subfamily, forest type, mean base-line corrected $\delta^{15}N$ isotope values in the respective habitats, and the (maximal) difference. Numbers under "Forest type" give sample size (A: alluvial, L: limestone, D: dipterocarp and K: Kerangas). T-value given from the statistical analyses with T-tests, as well as degrees of freedom (df) and statistical significance (p). [1]Since *Camponotus gigas* was collected in three forest types with a sufficient sample size, we calculated an ANOVA ($F_{2,14} = 12.47$; $P > 0.001$), the $\delta^{15}N$ values differed as follows: mean alluvial = 2.16; mean limestone = 2.99; mean Kerangas = 3.41;. unequal N HSD post hoc test $p < 0.05$ for A vs. L and K, but not for L vs. K).

Species	Subfamily	Forest type				Mean $\delta^{15}N_{cor}$	Mean $\delta^{15}N_{cor}$	Diff. (max)	t-value	df	p
		A	L	D	K	Habitat 1	Habitat 2				
Technomyrmex lisae	Dolichoderinae	7	4			3.01	4.06	1.05	-3.93	9	*0.003
Camponotus gigas[1]	Formicinae	5	5		7			1.25		14	[1]*0.001
Odontomachus rixosus	Ponerinae	4		5		5.55	5.72	0.17	0.36	7	n.s. 0.731
Acanthomyrmex ferox	Myrmicinae	5		5		4.45	5.63	1.18	-1.54	6	n.s. 0.174
Crematogaster sp. 9	Myrmicinae		3		3	3.67	6.60	2.93	5.72	4	*0.005
Lophomyrmex bedoti	Myrmicinae		11		4	4.61	5.55	0.94	3.27	13	*0.006
Lophomyrmex longicornis	Myrmicinae	6	4			4.67	5.38	0.71	-0.93	8	n.s. 0.379
Tetramorium sp. near *vertigum*	Myrmicinae	5			3	4.88	6.22	1.34	-2.90	6	*0.027
Pheidole quadrensis	Myrmicinae	5		4		4.99	5.52	0.53	-1.23	7	n.s. 0.256

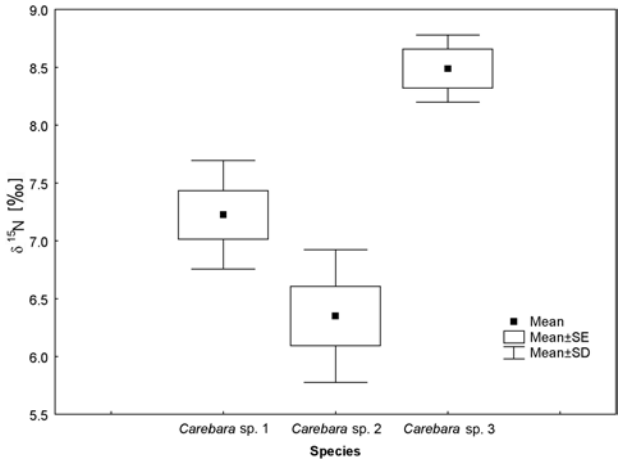


Fig. 7: Distribution of $\delta^{15}N$ values in ant species of the myrmicine genera *Carebara*. Sample size (n = number of samples analysed): *Carebara* sp. 1 (n = 5), *Carebara* sp. 2 (n = 5), *Carebara* sp. 3 (n = 3). All means were significantly different ($p < 0.05$) Unequal N HSD post hoc test after ANOVA (see Tab. 3).

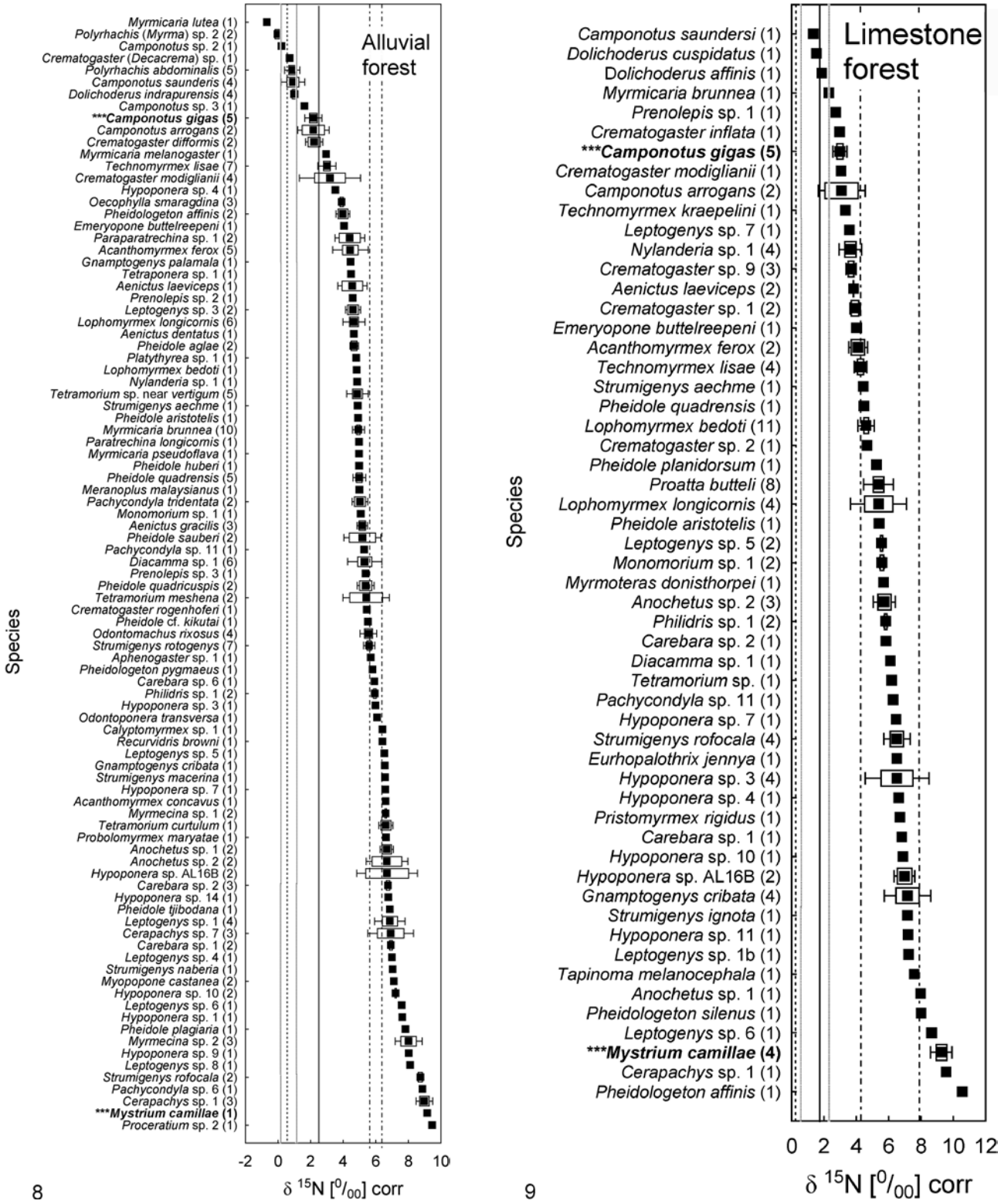
Leptogenys sp. 3 ($\delta^{15}N_{cor} = 4.57$, $p = 0.013$). All tested species of *Carebara* differed from each other (Fig. 7). However, in nine tested species of *Pheidole* we found significant differences only for *P. quadrensis* ($\delta^{15}N_{cor} = 5.15$) vs. *P. parvicorpus* ($\delta^{15}N_{cor} = 6.92$, $p = 0.018$). *Strumigenys rofocala* ($\delta^{15}N_{cor} = 7.38$) differed from *S. aechme* ($\delta^{15}N_{cor} = 4.60$) ($p = 0.004$) and *S. rotogenys* ($\delta^{15}N_{cor} = 5.59$) ($p = 0.005$). Furthermore we checked another nine species pairs for within-genera differences of $\delta^{15}N_{cor}$ values with independent t-tests and found significant differences in two species pairs: *Polyrhachis abdominalis* ($\delta^{15}N_{cor} = 0.87$) vs. *Polyrhachis nigropilosa* ($\delta^{15}N_{cor} = 2.90$, $t = -5.11$, $df = 5$, $p = 0.004$) and *Paratrechina longicornis* ($\delta^{15}N_{cor} = 5.47$) vs. *Paratrechina* sp. 1 ($\delta^{15}N_{cor} = 4.04$, $t = -5.11$, $df = 5$, $p = 0.004$).

Food chains in the four forest types. We assessed 93 ant species from alluvial forest, 55 ant species from limestone forest, 42 ant species from the Kerangas and 64 ant species from dipterocarp forest (Figs. 8 - 11). In alluvial forest (Fig. 8), $\delta^{15}N_{cor}$ of the studied species ranged over 10.15‰ (median = 5.36‰ $\delta^{15}N$, variance = 4.39), corresponding to 3.4 steps in the food chain. In limestone forest (Fig. 9), $\delta^{15}N_{cor}$ of ant species ranged over 9.21‰ (median = 5.58‰ $\delta^{15}N$, variance = 4.21), corresponding to 3.1 steps in the food chain. In dipterocarp forest (Fig. 10), $\delta^{15}N$ of the studied species showed a range over 7.64‰ (median = 6.30‰ $\delta^{15}N$, variance = 3.22), representing 2.5 steps in the food chain. In the Kerangas (Fig. 11), $\delta^{15}N$ of the studied species ranged over 6.84‰ (median = 6.22‰ $\delta^{15}N$, variance = 2.84), equivalent to 2.3 steps in the food chain. However, when we tested for differences in the variance of transects' mean $\delta^{15}N$ values, we found no significant differences between transects, indicating that transect length was equal (R, stat package, F-tests, smallest $p = 0.11$, see Appendix S5). Moreover, differences between the shared species with lowest (*Camponotus gigas*) and highest $\delta^{15}N$ (*Mystrium camillae*) values were small: alluvial forest = 6.99‰, limestone forest = 6.27‰, dipterocarp forest = 6.71‰, and Kerangas = 6.20‰.

When we compared $\delta^{15}N$ values (base-line corrected) of the nine ant species which were collected with an adequate sample size in several forest types ($n \geq 3$ in each forest type), $\delta^{15}N$ values of five species differed significantly between two forest types (Tab. 4).

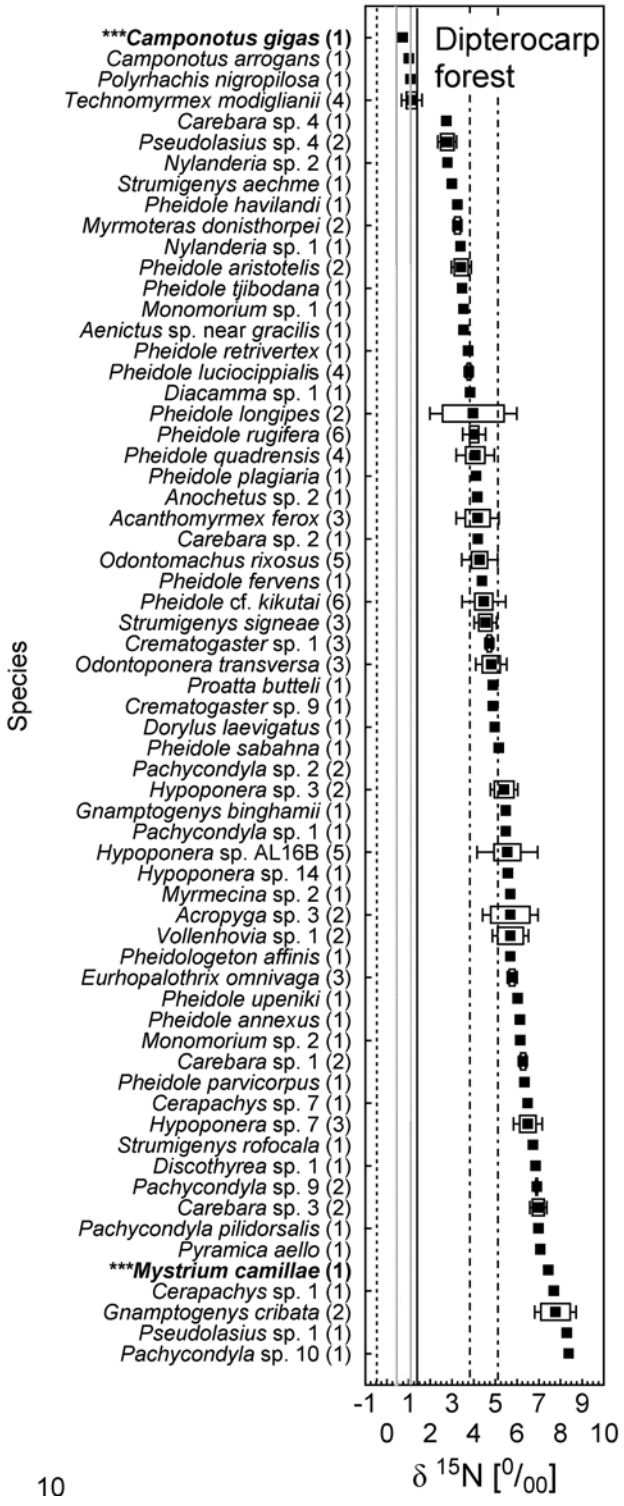
Discussion

Trophic modes of ground-dwelling ants. Our results clearly indicate that ground ant communities are not dominated by predators, but show a wide range of trophic modes, with

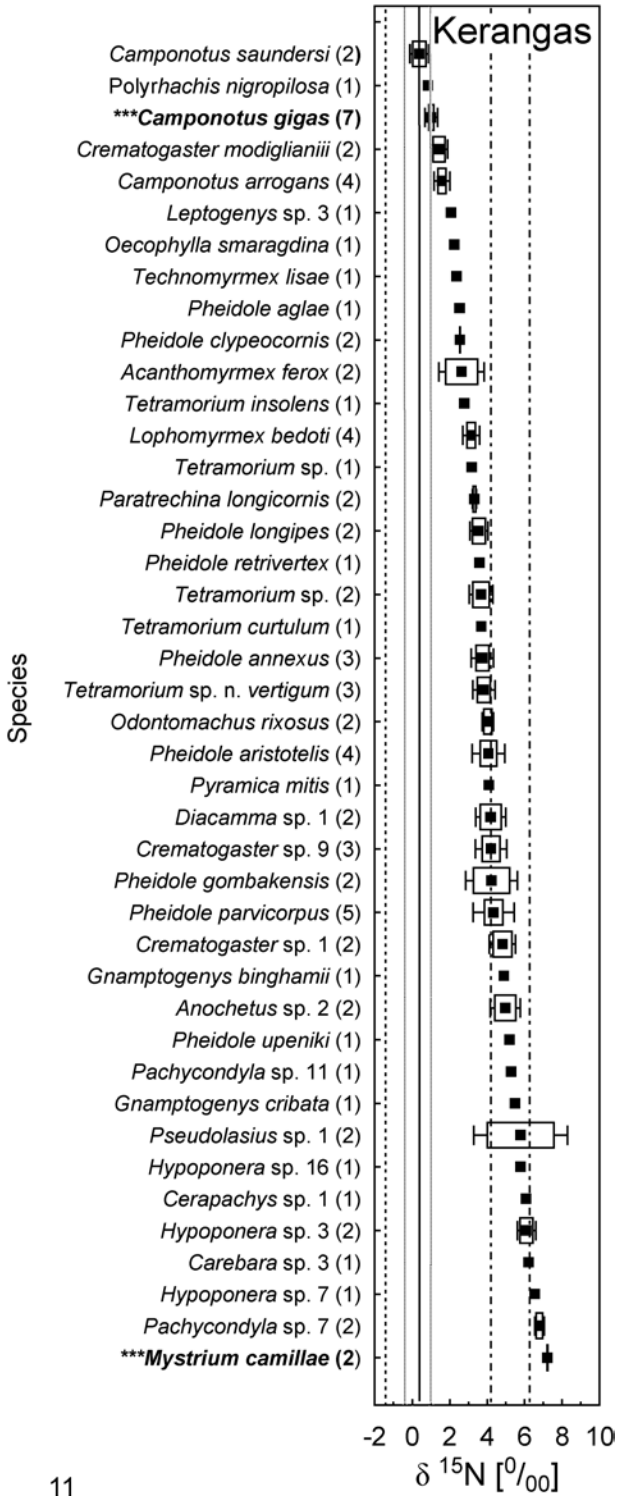


Figs. 8 - 11: δ ^{15}N values of ant species of the four forest types investigated in Gunung Mulu National Park: (8) alluvial forest, (9) limestone forest, (10) dipterocarp forests and (11) Kerangas. Common species with the lowest δ ^{15}N values (*Camponotus gigas*), and with the highest δ ^{15}N value (*Mystrium camillae*) of the respective food chains are marked. δ ^{15}N values are base-line corrected for those forest types with two transects: limestone and alluvial forest. The regular dashed line represents the N-signature of the leaf litter, while the straight line shows the isotope signature of the topsoil. The range of the herbivore and carnivore arthropods for reference is the range between the fine dotted lines (herbivores) and irregular large dashed lines (carnivores). Sample size is given in parenthesis after the species name.

For alluvial forest and limestone forest base-line corrected values are given, as these specimens have been sampled at two distinct transects, for which we have corrected. For dipterocarp forest and Kerangas we present uncorrected values.



10



11

Figs. 10 - 11: Legend see p. 37.

$\delta\ ^{15}N_{cor}$ values of the studied species ranging over 11.23‰, corresponding to 3.7 steps in the food chain. As has been reported previously from studies based in other ecosystems and habitat layers (BLÜTHGEN & al. 2003, DAVIDSON & al. 2003, FIEDLER & al. 2007), ground ant communities of all forest types showed a continuum of $\delta\ ^{15}N$ values and even a unimodal, almost normal distribution of the $\delta\ ^{15}N$ values in at least three of the four forest habitats (see Appendix S6).

Although we can separate three trophic modes, "herbivores", "omnivores", and "predators" by comparison with the arthropod samples and using the conclusions of FELDHAAR & al. (2009), the transitions between these dietary preferences are seamless, and omnivory was preferred by most species.

The "herbivores" were species mostly of *Polyrhachis* and *Camponotus* with low $\delta\ ^{15}N$ values resulting from the use of carbohydrate-rich exudates from hemipterans

(BLÜTHGEN & al. 2006) and other plant-derived food sources such as EFNs (BLÜTHGEN & al. 2003). While they represent the most species-rich group in the vegetation layer (DAVIDSON & al. 2003), in leaf litter and soil this group was represented by only a few species, which nested on the ground and foraged both on the ground and in the vegetation, like the Giant Forest Ant *C. gigas* (PFEIFFER & LINSENMAIR 2007). Two studied *Polyrhachis* species differed significantly in their isotope values, which is in contrast to the general assumption that most *Polyrhachis* species have a quite uniform diet (BLÜTHGEN & FELDHAAR 2009) and stresses the need for further nutrition studies on this most species-rich ant genus of the region (PFEIFFER & al. 2011).

Some ground ants like *Pseudolasius* keep trophobionts (MALSCH & al. 2001), but for these ants the hemipteran exudates seemed to be only a minor food source because their high $\delta\ ^{15}N_{cor}$ values were indicative of a more predacious lifestyle. Such ants, mostly in the subfamilies Formicinae, Dolichoderinae, Myrmicinae, and Ponerinae, were classified as "omnivores" comprising species with mixed diets and opportunistic lifestyles.

The third trophic group consisted of truly predacious ants, such as species of Aenictinae, many Ponerinae, Ectatomminae, Cerapachyinae, and Amblyoponinae, some of which exhibit a degree of prey specialisation (BOLTON 2000). This included ants which prey on other predatory arthropods like the amblyoponine species *Mystrium camillae*, a species with one of the highest measured $\delta\ ^{15}N_{cor}$ values, which specialises on centipedes (BROWN 2000). Even at subfamily level prey specialisations can be demonstrated. For predacious ants the Aenictinae had quite low $\delta\ ^{15}N_{cor}$ values, reflecting the fact that *Aenictus* species mostly hunt other ants like *Camponotus*, *Polyrhachis*, or *Dolichoderus*, of the lowest trophic group (ROŚCISZEWSKI & MASCHWITZ 1994, HIROSAWA & al. 2000). These results were corroborated by analysis of the $\delta\ ^{13}C_{cor}$ values of both prey and predator genera (M. Pfeiffer, D. Mezger & J. Dyckmans, unpubl.). Species of the genus *Cerapachys* are predators of larvae of other ant species (HÖLLDOBLER 1982); their high $\delta\ ^{15}N_{cor}$ values indicated that they probably hunted litter ants like cryptic species or specialised predators.

As indicated by the differing slope of isotope values in Figures 8 - 11, the number of species in the different trophic groups varied strongly: Few species were found at the lower or higher ends of the "food chain"; most species could be attributed as omnivores, with different levels of trophic overlap found in each of the forest types, possibly because of different resource supply in the forests. Diversity of species within a genus differed among forest types, e.g., for the genus *Strumigenys* we found 14 species both in alluvial and limestone forest, but only eight species in dipterocarp forest and four species in the Kerangas. Differences of the $\delta\ ^{15}N_{cor}$ values between different *Strumigenys* species suggest that these species specialise on certain types of prey (BOLTON 2000, MEZGER & PFEIFFER 2010a) and forest types may differ in the availability of prey types. In contrast, between 11 and 18 species of *Pheidole* were found in the various forests, but $\delta\ ^{15}N$ values hardly differed between species. In *Pheidole* niche differentiation according to temperature has been demonstrated (MEZGER & PFEIFFER 2010c), but less information is available on differences in prey specialisation. Future inclusion of $\delta\ ^{13}C$ values in trophic studies of ants are needed to better separate trophic niches of sympatric species.

Impact of phylogeny and calibration. Our analysis corroborated our second and third hypotheses that stressed the impact of phylogeny on trophic structure of the studied ant communities. Subfamilies of ants could be separated according to their base-line corrected $\delta\ ^{15}N$ values, although some groups were not distinct in the post hoc tests, probably due to lower sampling effort. Moreover, some genera could be statistically significantly separated within subfamilies, and species within genera, thus pointing towards dietary preferences as an important evolutionary force for speciation. Our results illustrate the evolutionary history of ants which is closely connected to the evolution of their food preferences from predation to herbivory, starting with the radiation of ants during the Late Cretaceous (WILSON & HÖLLDOBLER 2005, MOREAU & al. 2006). The most ancient tested subfamilies, Proceratiinae and Amblyoponinae, both specialised predators, fall in the group with highest $\delta\ ^{15}N_{cor}$ values, while subfamilies that evolved later show more omnivorous tendencies. Situated at the lower end of the food chain, Formicidae and Dolichoderinae comprise herbivore species depending on trophobiotic interactions with plant-sucking insect groups that developed after the rise of the angiosperms (TOBIN 1994, DAVIDSON 2003). This adds to our current knowledge on trophic ant ecology and corroborates former studies, some of which have been produced with much lower sample size (overview in BLÜTHGEN & FELDHAAR 2009).

Although the exact $\delta\ ^{15}N$ values for the single taxa cannot be directly compared with other studies because baselines are differing (FIEDLER & al. 2007) (and most other studies present data in figures rather than in tables) the fundamental data match well with the above mentioned trophic order of subfamilies and genera. This is largely true also for the Asian data of DAVIDSON & al. (2003), which were gathered in Brunei, only 50 kilometers from our sample site in Sarawak. Twenty species are shared between both studies; however, the lack of a common base-line makes it difficult to compare the studies.

The impact of a correct calibration has been recently stressed by WOODCOOK & al. (2012), who argue for small scale calibration with base-lines not further than 500 m apart. In our study this has been done for each of the transects with samples of subsoil and leaf litter directly from the Winkler plots as recommended by CHAHARTAGHI & al. (2005). These items make up the environment inhabited by ground ants and should have an immediate impact on organisms' stable isotope patterns at that sample point.

Correct calibration is necessary to address the question as to whether different habitats affect $\delta\ ^{15}N$ values of species. From nine species inhabiting two or more forest types, five differed significantly in their $\delta\ ^{15}N$ value between habitats, indicating different diets that might be caused by different levels of competition or different food availability. Certain other species differed strongly among forest types – with and without calibration (e.g., *Pheidologeton affinis* with a range from $\delta\ ^{15}N_{cor}$ of 3.99 (alluvial, n = 2) to 10.56 (limestone, n = 1)). These results reflect the adaptability of ants to habitat conditions and demonstrate that niche patterns of certain species may change depending on nutrient availability and competition, as has been shown for predators (including ants) in agroecosystems (DUYCK & al. 2011).

Although total length of the food chain was strongly variable in different forest types, the similar variances indicate that this is a sampling artifact due to differing sam-

ple sizes. Kerangas, the type with the shortest food chain, had the smallest sample coverage (Tab. 1) and this may well explain the observed differences.

Conclusion

Our study demonstrates the large dietary variability in the Formicidae. Stable isotope measures of $\delta^{15}N$ values are an appropriate tool to assess the feeding habits of these important soil arthropods, which are often cryptic in both their behaviours and dietary preferences. More studies with an even narrower grid of base-lines are necessary to study the flexibility of ant food choice and trophic status among habitats.

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