

Diet Specialization in Central American Army Ants

**Ernährungsspezialisierung von zentralamerikanischen
Treiberameisen**

Julius-Maximilians-Universität Würzburg

Fakultät für Biologie

Lehrstuhl für Tierökologie und Tropenbiologie



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eingereicht von Philipp O. Hönle

aus Leonberg

Matrikelnummer: 1894567

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Erstprüfer:

Akad. Direktorin Dr. Brigitte Fiala (Universität Würzburg)

Zweitprüfer:

Dr. Christoph von Beeren (Technische Universität Darmstadt)

Einreichungsdatum:

Affidavit

I hereby confirm that my thesis entitled 'Diet Specialization in Central American Army Ants' is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

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Abstract

Army ants are top arthropod predators in tropical ecosystems. During their daily mass raids thousands of army ant workers roam the forest in search for living prey, inferring strong top-down effects on their prey. Despite their important ecological role, little is known about the diet of most army ant species. I conducted a large-scale diet assessment of army ant species in a Neotropical community known to have a particularly high army ant density, i.e. that of La Selva Biological Station (Costa Rica). Over a period of nine weeks, I collected prey items of eleven surface-raiding army ant species belonging to three genera: *Eciton*, *Nomamyrmex* and *Neivamyrmex*. I noted exact location and time of the raid and identified adult prey morphologically and immature prey via DNA barcoding. Altogether, I collected more than 3200 prey items from 233 raids. The prey nearly exclusively consisted of other ants (98%), and most prey items were brood (87%). Several predator-prey network analyses revealed a high degree of diet specialization among army ant species, and their food niches differ significantly from each other. Furthermore, I also noted a temporal and spatial (ground vs. canopy raiders) differentiation among the studied species by indirectly inferring the raiding stratum through the preferred nesting habits of each ant prey species. Prey specialization was found to be neither correlated with army ant phylogeny nor with army ant abundance. My results suggest that an important ecological factor facilitating the coexistence of diverse army ant communities is a differentiation in their food niche.

Zusammenfassung

Treiberameisen sind hochrangige Prädatoren in tropischen Ökosystemen. Während ihrer täglichen Raubzüge durchstöbern tausende von Treiberameisen den Waldboden auf der Suche nach lebendiger Beute und beeinflussen so Beutepopulationen stark. Trotz ihrer wichtigen ökologischen Funktion ist nur wenig über ihre Ernährung bekannt. In einer Region die für ihre hohe Treiberameisendichte bekannt ist, La Selva (Costa Rica), habe ich eine großangelegte Studie über die Treiberameisenbeute durchgeführt. Während der Studiendauer von 9 Wochen wurde die Beute von elf Treiberameisenarten aus folgenden drei Gattungen systematisch abgesammelt: *Eciton*, *Neivamyrmex* und *Nomamyrmex*. Dabei wurde

immer die exakte Position und Zeit des Raubzugs aufgenommen. Die adulten Beutestücke wurden anschließend morphologisch auf Artniveau bestimmt, und die Brut mithilfe von DNA Barcoden identifiziert. Insgesamt wurden mehr als 3200 Beutestücke von 233 Raubzügen abgesammelt. Diese Beute bestand fast ausschließlich aus anderen Ameisen (98%), vor allem in Form von Brut (87%). Räuber-Beute Netzwerkanalysen zeigten, dass die Treiberameisen hochspezialisiert sind, und es nur geringe Überlappungen im Beutespektrum gab. Außerdem ergab sich, dass sich die Ameisen in ihrer Raub-Aktivitätszeit und ihrem bevorzugten Furagierstratum (auf Bäumen oder dem Boden) unterschieden, wobei letzteres indirekt über die bevorzugte Nistweise der Beuteameisen ermittelt wurde. Die Beutespezialisierung war weder mit phylogenetischer Divergenz noch mit der Abundanz der Treiberameisen korreliert. Meine Ergebnisse deuten darauf hin, dass eine Differenzierung der Nahrungsnische ein wichtiger ökologischer Faktor ist, welcher die Koexistenz von Treiberameisenarten fördert.

1 Introduction

Ants (Formicidae) are among the most abundant organisms in nearly all terrestrial habitats (Lach et al. 2010). Within the arthropod community they represent one of the largest group of scavengers, omnivores, predators and herbivores, which makes them important components of many ecosystems (Hölldobler & Wilson 1990). Especially their top-down effects on insect prey are large, and as such they play an important role for natural ecosystem functioning as well as for human agrosystems (Elmes 1996; Philpott & Armbrecht 2006; Rosumek et al. 2009).

The most conspicuous predators among ants are the army ants, which have sparked intensive interest since their discovery by researchers travelling in the tropics (e.g. H.W. Bates 1863). The impact of army ant raids on tropical arthropod communities is considerable. For instance, the daily raided arthropod prey biomass in *Eciton hamatum* was estimated to be 120g/km² (Powell 2011). Reaching surprisingly high abundances in local communities, they probably rank among the animals with highest trophic position in certain tropical ecosystems (Rettenmeyer et al. 1983; Gotwald 1995; O'Donnell et al. 2009). Besides their important ecological role as predators, they attract a wide variety of associates such as ant birds and many arthropod myrmecophiles (Wrege et al. 2005; Parker 2017). In fact, the over 300

associated myrmecophile species of *E. burchellii* represents the largest known species association focused on a single animal species (Rettenmeyer et al. 2010). The ecological function of army ants is therefore a vital aspect of conservation, especially in regard to the current destruction and fragmentation of natural habitats by humans. They are thought to be one of the keystone species, and their limited dispersal abilities might put them under threat (Boswell et al. 1998; Peters et al. 2008).

A lot of research has focused on army ants in the recent decade alone, entangling their taxonomy (Borowiec 2016), phylogeny (Borowiec 2017), reproductive mode (Kronauer et al. 2011), and certain ecological traits (Kaspari & O'Donnell 2003; Kaspari et al. 2011). An 'army ant' is, however, not a monophyletic taxon but rather a merged entity of ants that share several characteristics, which are denoted as the 'army ant syndrome' (Gotwald 1995). These characteristics are a specialized queen caste without wings ('dichthadiigyne'), mass foraging, and frequent colony migrations (Gotwald 1995; Brady 2003). Furthermore, a striking characteristic, which is however absent in some genera (e.g. *Dorylus*), are synchronized brood cycles that result in alternating colony migration phases (Schneirla 1971; Garnier & Kronauer 2016). One can distinguish between the 'true' army ants (e.g. *Eciton*), their more basal relatives within the Dorylinae (e.g. *Oocera*) and convergently evolved army ants in the wider sense, e.g. some species of *Carebara* (Moffett 1988) or *Leptogenys* (Maschwitz et al. 1989). Over a long period of time, there were ongoing discussions whether the 'true' Old World and New World army ants represent two convergently evolved taxa or whether the true army ants share a common ancestry (Gotwald 1979; Kronauer 2009; Brady et al. 2014). The most recent study about this topic suggests that both hypotheses are true: All true army ants form a monophyletic taxon within the subfamily Dorylinae but evolved their army ant syndrome convergently in the New- and Old World (Borowiec 2017). To avoid confusion, whenever mentioning army ants in this thesis, I specifically mean 'true' army ants, i.e. the New World genera *Eciton*, *Neivamyrmex*, *Cheliomyrmex*, *Labidus* and *Nomamyrmex* and the Old World genera *Dorylus*, *Aenictus* and *Aenictogiton*. These taxa have received different scientific attention. Some species of the suspicious *Eciton* and *Dorylus* are quite well known, some other army ants have been mostly neglected and their biology is basically unknown (see Borowiec 2016).

While many aspects of army ants have been disentangled in recent years, the basic ecology of most species remains poorly studied. This study aims to address the diet preferences of army ants to better understand their role in tropical ecosystems. Their primary ecological impact is mediated via predation. During their raiding activities, several thousand foragers leave their nest in columns for search of prey, eventually returning it to their nest. One can broadly distinguish between swarm and columns raiders: The swarm raiders build up a swarm front that is several dozens of meters wide and slowly crawls across the leaf litter in search for prey, while the column raiders have smaller, branching trails (Schneirla 1971). There are many studies showing that army ants seem to rely mostly on other social insects (primarily ants) as prey (Rettenmeyer et al. 1983; Powell & Baker 2008). However, information about the ecological niches of army ants are mostly anecdotal or focus on single species, and very rarely consider army ant communities (a notable exception are Asian *Aenictus*; Rosciszewski & Maschwitz 1990; Hirose et al. 2000; Hashimoto & Yamane 2014). As a tropical habitat can contain up to 20 army ant species, the question arose how so many “top predators” can co-exists in one area (Hölldobler & Wilson 1990). Competition driven niche specialization is thought to be an important driver behind species co-occurrence (Pianka 1974), and is thought to increase resource exploitation (Finke & Snyder 2008). One of the most limiting factors for army ants is likely their diet, which is why specialization within the scope of this thesis is defined from a dietary perspective. Within a community of army ants, a high level of dietary specialization would therefore be expected.

In the present master thesis, I addressed this hypothesis by surveying the predation networks of 11 sympatric army ant species with, as revealed in my study, >120 prey species at “La Selva Biological Station”, Costa Rica. With the help of field assistants, I systematically collected the prey of army ants to assess their diet spectrum and to determine the level of diet specialization of the community. I therefore identified the prey items to the species level via morphological identification. However, a considerable part of the prey consisted of immature stages of ants, which are difficult to identify as there are no available keys. For these prey items, I used the classical animal barcode marker *cytochrome oxidase I* (from here on abbreviated as *COI*) to determine species identities. This was only feasible because a large *COI* reference database of properly identified Costa Rican ants existed (BOLD 2017). As reported by anecdotal

observations (Rettenmeyer et al. 1983; Powell & Bakers 2008), I expected to find high degrees of diet specialization among sympatric army ant species. I also expected to find temporal niche partitioning among army ants to avoid direct competition as shown previously (O'Donnell et al. 2009). Furthermore, using the nesting habits of their prey, I expected to find differences in spatial niche use (i.e. ground and arboreal raiders) of different army ant species. Taken together, I expected to find differentiation in several niche parameters within the army ant community at La Selva, which might help to explain the coexistence of a high diversity and density of army ants at La Selva.

2 Materials and Methods

2.1 Field sampling

The study was carried out in the Costa Rican tropical wet forest at La Selva Biological Station (N10 25.847 W84 00.404). The research area was approximately 11 km² including primary and secondary forest segments (for a map of La Selva see Supplement S1). Samples were collected from the end of February 2017 to the end of April 2017. Together with Bryan Ospina Jara, my Colombian field assistant, I searched for army ant raids by walking along the extensive trail system at La Selva. I searched for army ants between 9 pm and 3 am during the night and between 4 pm and 5:30 pm during the day, as these were typical raiding activity periods (von Beeren, pers. comm.). Army ants are central place foragers and transport all of their prey to their nest before prey is consumed by their larvae. Prey items and army ant workers were thus collected during army ant raids and during colony emigrations, from which I collected the first 10 prey items that I encountered with forceps. Sometimes army ant establish a temporary prey storage (henceforth called "prey cache"). If such a prey cache was encountered, a larger random sample of 20-40 prey items was taken. So, whenever I collected prey items I only rarely observed the direct raids, but focused on collecting returning foragers with prey. I recorded the exact coordinates and the collection time with a handheld Garmin GPS. The samples of both army ant and their prey were immediately stored in 2ml vials containing absolute ethanol (VWR chemicals).

I aimed to minimize re-sampling of the same army ant colony. Hence, during that same day,

raids of the same species within a radius of ~50 m of the last sampling spot were neglected. One exception was made for the very rare *Eciton lucanoides*. When encountering this species, we sampled from both raid columns and colony emigrations to increase the sample size of prey items. I thus know that I have several samples of *E. lucanoides* collected from the same colony and this might be also true for other species. In fact, it is difficult to avoid re-sampling of the same colony entirely due to the migratory habit of these ants. Note that the aim of the present study was to evaluate the prey spectrum of different army ant species. I thus do not expect that occasional re-sampling of the same colony on different days has a strong effect on the results, i.e. diet preferences of different army ant species.

2.2 Identification and Molecular Protocol



Fig. 1 Example of prey items collected from one *Eciton hamatum* raid (collection ID: EH33). 1-9 *Acromyrmex* brood; 10, 11: polistine Wasp; 12 & 13: *Neoponera villosa*. Scale bar in millimeter.

Previous to any identification, I took a photograph of all samples of all raid items for each collection on a black or white paper using a Nikon D5300 SLR and assigned each prey item a unique identification code (Fig. 1). For each raid sample, I then mounted the army ant species as well as the adult prey items, which are vouchered at Christoph von Beeren's personal collection. I focused on ant prey and did not further identify non-ant prey. The ants were

identified with available taxonomic keys (army ants: Watkins 1976; army ants and prey ants: Longino 2010). Brood items were sorted morphologically and, if possible, identified to genus or subfamily level. The developmental stage (i.e., egg, larva, pupa or adult) was noted for each ant prey item. A large part of the collected prey was ant brood, for which I primarily relied on DNA barcoding to identify species.

I took representative samples of each 'brood morphospecies', about 1-10 per raid. A morphospecies was defined as larvae or pupae that looked very similar to each other anatomically. The DNA of individual prey items was extracted in 96-well plates using the QIAGEN 96 DNA Easy Tissue kit. The extraction followed standard protocol instructions. With the use of standard polymerase chain reaction (PCR), I amplified a fraction of the mitochondrial gene *COI* using several primers: LCO1490/HCO2198 (Folmer et al. 1994) and LepF1/LepR1 (Herbert et al. 2004). A standard thermocycling profile was used with initial denaturation steps of 5 min at 95 °C followed by 40 cycles of 94 °C for 30s, 47 °C for 30 s, and 72 °C for 90 s, followed by 10 min at 72 °C. Using standard gel electrophoresis, the samples were tested for successful DNA amplification. If this was case, they were send for sequencing to Macrogen Inc. Europe. I sequenced the *COI* fragment in forward and reverse direction. In case of low quality reads, samples were re-sequenced with different primers. The respective forward and reverse sequences were assembled with the MUSCLE algorithm and trimmed with the software Geneious (version R11.03). Consensus sequences were then compared to online reference databases for *COI* to acquire species identifications (BLAST 2017; BOLD 2017). Prey items with a good match to a record in the database (>98% sequence match) were assigned either species name or BOLD/BLAST sample ID (e.g. '*Camponotus* MAS008'). Prey items with a lower match (<98% sequence match) were assigned to genus level with closest match ID (e.g. *Gnamptogenys* sp. MAS010).

2.3 Raiding Stratum

For determining the level of stratum specialization for prey retrieval, I noted for each prey item a characteristic nesting stratum. I broadly distinguished between ground nesters and

arboreal nesters. The ground nesters include species that have their nest in leaf litter, in dead wood or underground. Species with arboreal nests range from lower arboreal zone up to the canopy. Because some ant species occur across both strata, I assigned them a third category of “both strata” nesters. I mainly used observations by Longino (2010) to determine the nesting stratum. Species for which nesting type was unclear were assigned to the category “Unknown”. The latter category provides no information about raid stratum and therefore excluded from the network analysis (see next section). The categorization for each taxon and the reference can be found in the Supplementary Material (Table S1).

2.4 Statistical Analysis

The statistical software R v3.1.2 in combination with RStudio v0.98.501 was used for statistical analysis and graphics (R Team 2016). To visualize diet specialization, I constructed an army ant-prey network using the R-package “bipartite”, with the army ants representing the higher trophic level and their prey ants representing the lower trophic level. My interaction network matrix was composed of incidence data (presence/absence) of prey species per raid to provide a robust network for missing identifications and varying sample size. For instance, I found 40 *Anochetus mayri* individuals in 10 different raids, so they had a total value of 10 in my interaction matrix. For characterizing bipartite networks a wide variety of indices is used. In my study, I used the H_2' for the whole network or d' for the species level (Blüthgen et al. 2006). H_2' values can range from 0 (no specialization) to 1 (highest specialization level). To test whether the resulting network significantly differed from a random network I created random null model networks with the Patefield method and compared these to the actual network (for details see Blüthgen et al. 2006). To test for a taxonomic preference by the army ant species, the network specialization was analyzed on three different taxonomic levels of the prey (subfamily, genus and species level). Because I was not able to identify all prey items on the species level, the sample size for each taxonomic level varies and is the lowest on species level. Similarly, the level of spatial niche specialization was calculated using network analysis and compared to a random null model as explained above.

Species accumulation curves with rarefaction were plotted with the R package “iNEXT” (Hsieh et al. 2016) and were based on incidence data per raid. For checking whether there were significant differences between developmental stage and activity time, I used a chi square test with significance level $\alpha=0.05$.

To test for a correlation between the diet and army ant phylogeny, I assembled two dendrograms. The diet similarity was calculated using the Bray Curtis similarity and the divergence data was taken from a well-resolved phylogeny of army ants (Winston et al. 2017). Because only data on divergence date of one *Neivamyrmex* species was available, I combined all three *Neivamyrmex* (*Ne. gibbatus*, *Ne. pilosus* & *Ne. asper*) to a single group. Both dendrograms were compared in a tanglegram using the R-package “dendextend” (Galili 2015), and the existence of a correlation between prey and phylogeny was tested with a Mantel test.

3 Results

3.1 Sample size and Composition

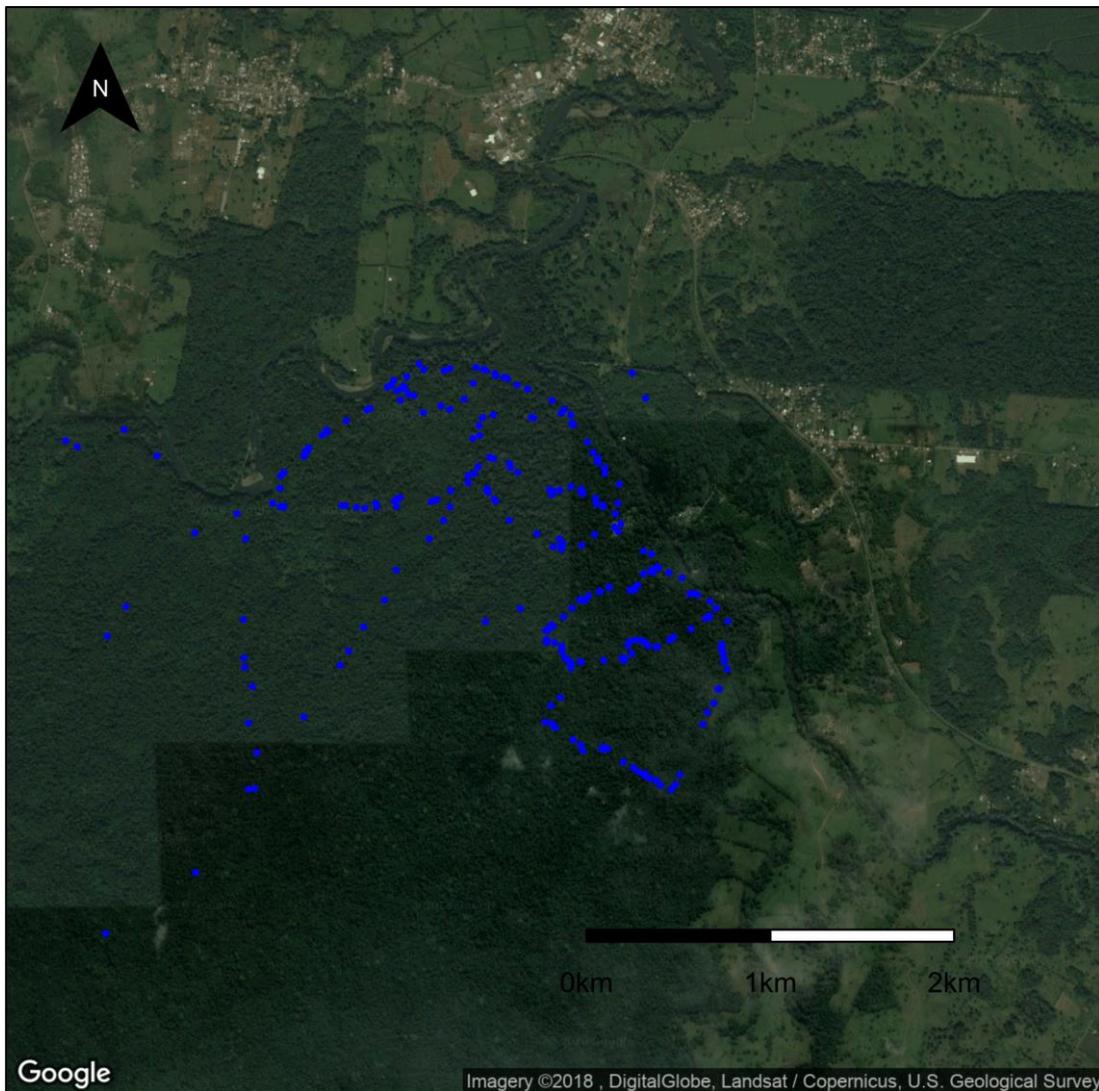


Fig. 2 Satellite pictures with blue dots indicating sampling points near La Selva Biological Station.

A total of 3,263 prey items were collected from 11 species of army ants. Of these, 98.5% consisted of ants, the remaining items were various arthropods (listed in Supplement S2). The exact number of raids, migrations and prey caches per species can be seen in Table 1, and their spatial distribution across La Selva is plotted in Fig. 2.

Table 1. Number and type of colony samples per species.

Species	Migrations	Raids	Prey caches	Total prey items
<i>Eciton burchellii</i>	4	36	1	467
<i>Eciton dulcium</i>	2	14	0	162
<i>Eciton hamatum</i>	6	14	7	530
<i>Eciton lucanoides</i>	4	4	1	126
<i>Eciton mexicanum</i>	3	35	1	436
<i>Eciton vagans</i>	1	48	1	782
<i>Neivamyrmex asper</i>	0	2	0	22
<i>Neivamyrmex gibbatus</i>	2	18	2	310
<i>Neivamyrmex pilosus</i>	0	22	0	268
<i>Nomamyrmex esenbeckii</i>	0	10	0	149
<i>Nomamyrmex hartigii</i>	0	1	0	10

I barcoded a total of 768 prey items, of which 435 were successfully amplified (57%) and resulted in a 658bp high quality read of the mitochondrial gene *COI*. Sequences are stored on several hard discs and will be submitted to GenBank as part of an upcoming publication, which is in preparation. Most of these prey items matched well to a record in the database (>98% sequence match in 77% of samples). However, many immature prey items of the genera *Acromyrmex* and *Camponotus* did not amplify well with the protocol used in this study.

Based on my sampling effort I estimated the coverage of prey species diversity for each species (Fig. 3). Accumulation curves indicated that, with >70% prey species coverage, I have a good representation of total prey diversity in *E. vagans*, *E. mexicanum*, *E. hamatum* and *E. burchellii*. For the other species, more intensive prey sampling is needed to reach a saturation in species accumulation curves. Note that the graph is based on identified species, unidentified prey items were not included.

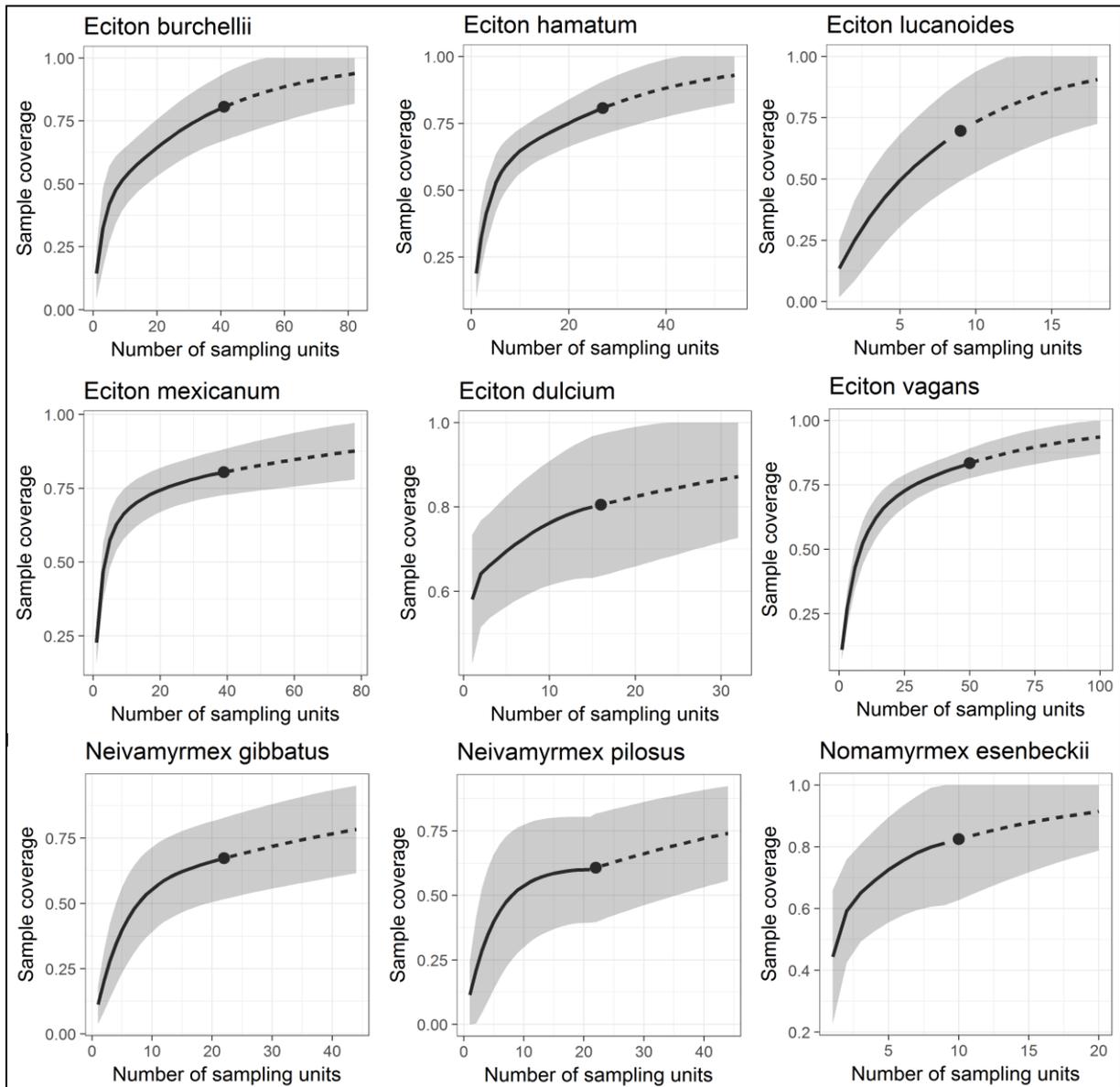


Fig. 3 Estimated prey sample coverage of each army ant species based on Hsieh & Chao (2016). Sample units are the total number of raids, migrations and caches. Black dot indicates estimated coverage with error margin (grey area, 95% confidence interval). Black line: Interpolation. Perforated line: Extrapolation.

The ant prey consisted of different developmental stages (egg, larva, pupa & adult), with the immature stages making up most of the prey. Pupae were the most common prey items (mean±SD: 52±14%) followed by larvae (mean±SD: 33±5%), adults (mean±SD: 14±16%) and eggs (mean±SD: 1±1%). The composition of development stages as prey varied across army ant species, except for larvae and eggs (adults $\chi^2=57.9$, $p<0.001$; eggs $\chi^2=5.9$, $p=0.65$; larvae $\chi^2=4.44$, $p=0.82$; pupae $\chi^2=24.1$, $p=0.002$). Most notably is that *E. dulcium* had a comparatively high relative amount of adult prey (~50%) in contrast to the other species which had few to

none adult prey items (Fig. 4). Eggs were rare and were only found in four *Eciton* species. In all army ant species pupae made up more than half of all prey items except in *E. dulcium*, where pupae made up 16% of total prey. Note that species with less than 5 collected raids were excluded from the analysis because of small sample size. Many ant pupae retrieved from army ants raids were nude pupae, i.e. not in a cocoon. Ant species from the subfamily Ponerinae, Ectatomminae and some Formicinae do not naturally have nude pupae, so their pupae were removed by army ant workers before reaching their nest. For instance, out of 232 Ponerinae pupae, 66% (n=154) had their cocoon removed, which occurred in all army ant species that raided on this subfamily.

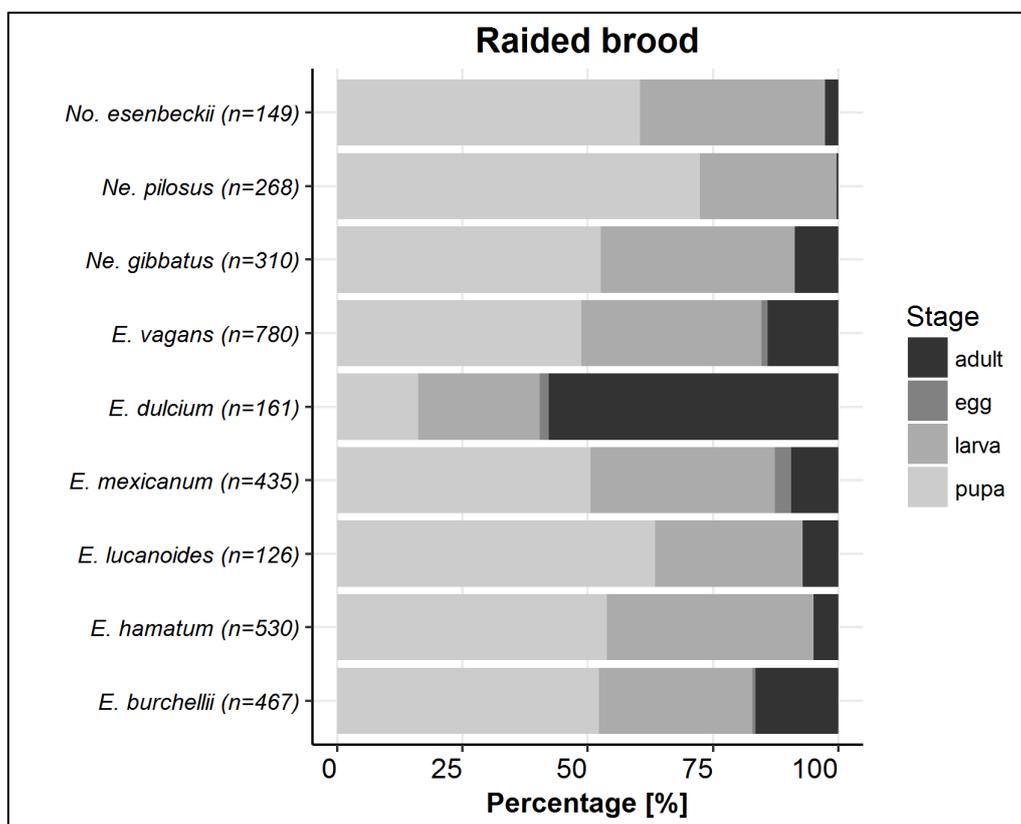


Fig. 4 Relative composition of the developmental stages of ant prey items. Colors indicate adult, egg, larva and pupal stages. Total number of ant prey items per species is shown in parenthesis.

3.2 Prey Specialization

Altogether I was able to identify 98.4% of ant prey on subfamily level. The resulting bipartite network has a network specialization index of $H_2'=0.29$, and is significantly different from a random network (Fig. 5; Patefield method, $p<0.001$).

Table 2 List of species level specialization (d') for each taxonomic level and army ant. *Nomamyrmex hartigii* has no d' on species level because I have no single prey species ID for this species. List of niche breath per species (Diversity + Shannon Diversity) including rarefaction and down sampling for $n=15$ species. Abbreviations: $S_{obs.}$: Diversity observed, S_{rare} : Species number estimated; $eH_{obs.}$: Shannon diversity observed; eH_{rare} : Shannon diversity estimated.

Species	d' subf.	d' genera	d' species	$S_{obs.}$	S_{rare} \pm SD	$eH_{obs.}$	eH_{rare} \pm SD
<i>E. burchellii</i>	0.41	0.61	0.74	14	8.3 \pm 1.2	8.6	6.2 \pm 1.3
<i>E. hamatum</i>	0.14	0.46	0.82	19	9.0 \pm 1.4	12.3	7.6 \pm 1.4
<i>E. lucanoides</i>	0.06	0.25	0.73	16	11.2 \pm 1.3	14.2	10.4 \pm 1.3
<i>E. mexicanum</i>	0.20	0.34	0.56	29	9.1 \pm 1.5	15.1	7.7 \pm 1.5
<i>E. dulcium</i>	0.36	0.50	0.56	8	5.9 \pm 0.8	4.1	3.6 \pm 0.8
<i>E. vagans</i>	0.09	0.37	0.52	39	11.2 \pm 1.7	25.4	10.3 \pm 1.7
<i>Ne. asper</i>	0.11	0.42	0.63	3	-	-	-
<i>Ne. gibbatus</i>	0.17	0.48	0.63	23	11.2 \pm 1.6	17.4	10.2 \pm 1.6
<i>Ne. pilosus</i>	0.34	0.92	0.95	8	8.0 \pm 0	5.9	5.9 \pm 0
<i>No. esenbeckii</i>	0.08	0.44	0.68	6	5.9 \pm 0.3	4.2	4.16 \pm 0.3
<i>No. hartigii</i>	0.00	0.33	-	-	-	-	-

I was able to identify 96% of ant prey items on genus level. The resulting network had an increase in specialization with $H_2'=0.53$ (Fig. 6; $p<0.001$). 67% of individual prey items could be identified on species level, but further DNA barcoding is likely going to increase this in the near future. The network level specialization was highest for the species level network ($H_2'=0.62$; Fig.7; $p<0.001$).

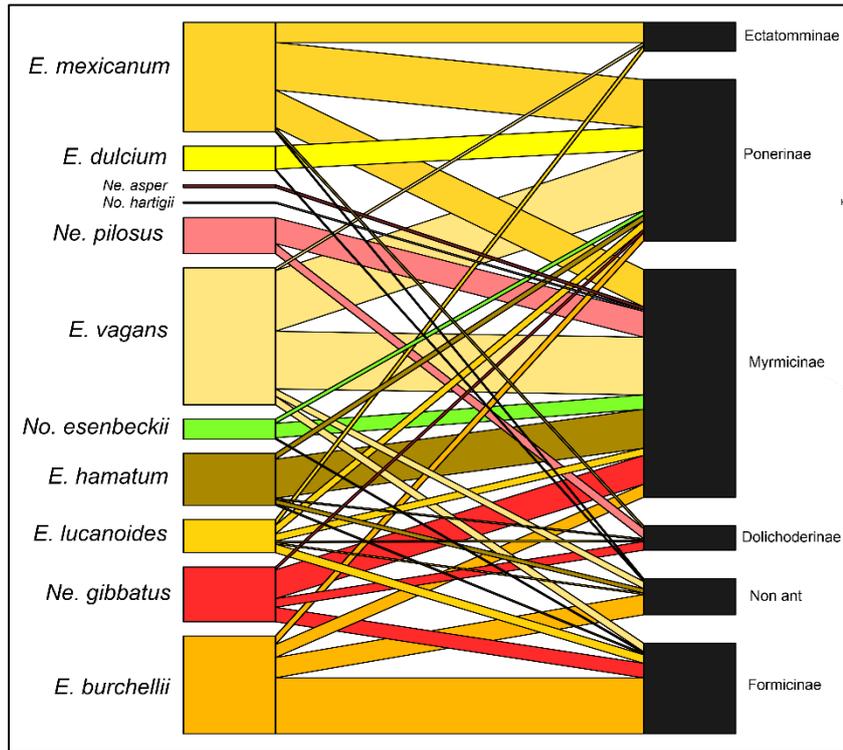


Fig. 5 Subfamily level specialization network. Yellow: *Eciton*; Red: *Neivamyrmex*; Green: *Nomamyrmex*

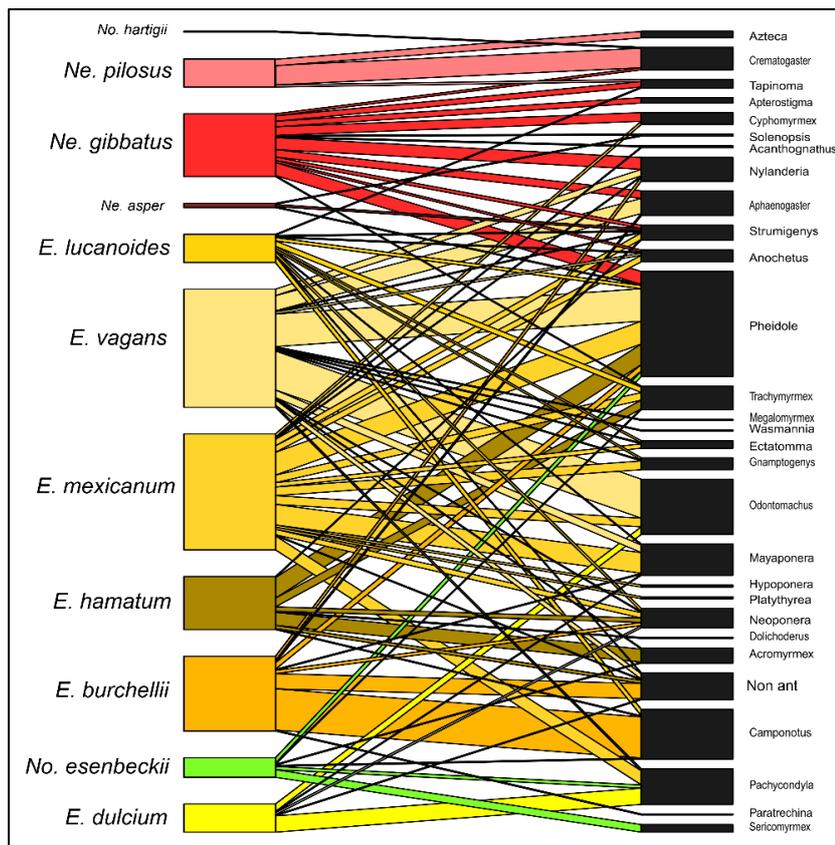


Fig. 6 Genus level specialization network. Yellow: *Eciton*; Red: *Neivamyrmex*; Green: *Nomamyrmex*

The most specialized army ant species is *Neivamyrmex pilosus* ($d' = 0.95$ on species level), and the most generalized species is *Eciton vagans* ($d' = 0.56$; Table 2). All species specialized on a different prey spectrum within in the network (all H_2' pairwise comparisons $p < 0.001$ except *Ne. asper* to *E. vagans*, *Ne. gibbatus* and *E. mexicanum*; Table S2). After accounting for sample size through rarefaction and down sampling, the prey diversity was highest in *E. lucanoides* (Shannon: 10.4 ± 1.3) and lowest in *E. dulcium* (Shannon: 3.6 ± 0.8), the average diversity had a Shannon index of 7.3 ± 2.1 species (Table 2). No intraguild (i.e. army ant- army ant) predation was observed in the studied species (but see Supplement Observation S4).

I tested for a correlation between species abundance (estimated as relative number of raids) and degree of specialization (d'), which was not significant (Spearman's Rank Test $\rho_s = -0.14$, $p = 0.70$). Furthermore, I tested for a correlation between the phylogeny of army ants and their prey composition, which was not detectable (Fig. 8, species level Mantel test on Spearman's rank correlation $p = 0.19$, genus level $p = 0.112$).

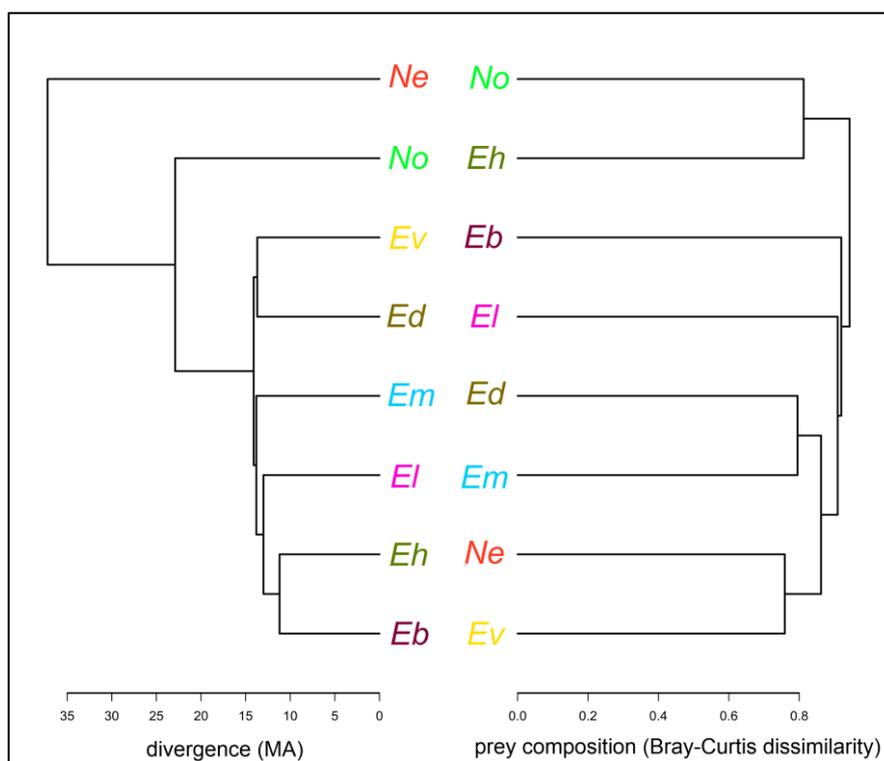


Fig. 8 Divergence time of army ants based on Winston et al. (2016) (left) compared to prey composition based on a Bray-Curtis dissimilarity matrix (right). Ne=*Neivamyrmex* spp., No=*Nomamyrmex esenbeckii*, Ev=*Eciton vagans*, Ed=*Eciton dulcium*, Em=*Eciton mexicanum*, El=*Eciton lucanoides*, Eh=*Eciton hamatum*

3.3 Spatial niche

The army ants showed different preferences for possible hunting grounds. This was indirectly assessed through the nesting type of their ant prey. There are species which hunt mostly arboreal (e.g. *E. burchellii* and *Ne. pilosus*; Fig. 9), and others that obtain their prey mostly from ground nesters (e.g. *E. dulcium* and *E. mexicanum*; Fig. 9). The according network has an $H_2'=0.22$ and differs significantly from a random network (Fig. 9; $p<0.001$).

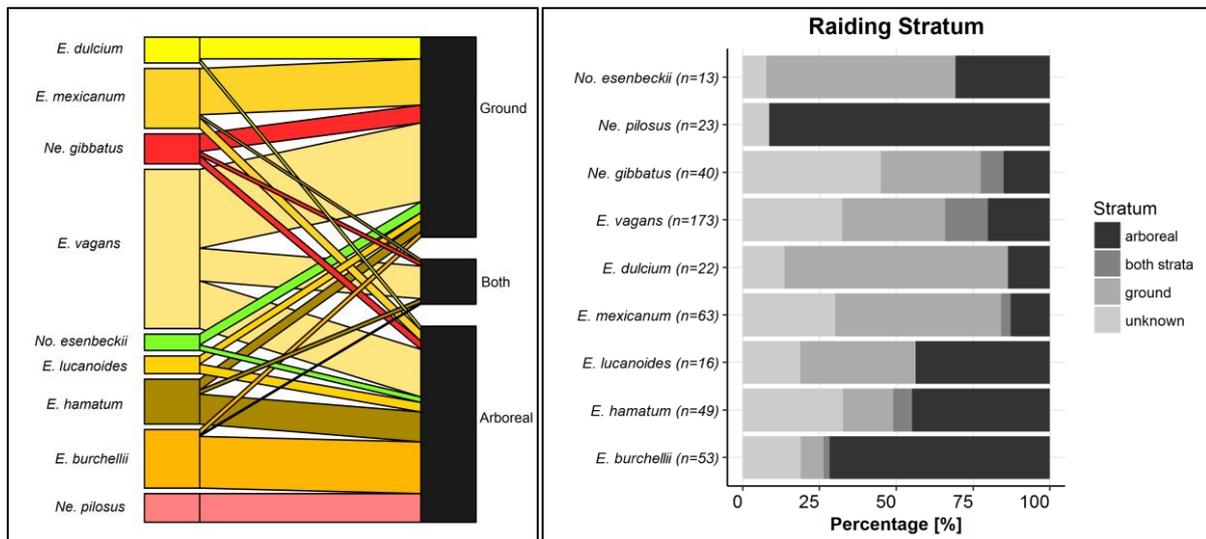


Fig. 9 Left: Network of stratum specialization for each taxon ('unknown' excluded). Yellow: *Eciton*; Red: *Neivamyrmex*; Green: *Nomamyrmex*. Right: The relative distribution of nest strata of ant prey across army ant species. Parenthesis indicate number of raids that contained prey of any stratum. Included in both graphs are only army ant species with $n>10$.

3.4 Activity patterns

Most army ant species showed preferences in their activity periods (Table 3). Two species can be classified as predominantly diurnal raiders, five species as nocturnal raiders and two species showed no preference in temporal raiding activity.

Table 3 Raiding activity period of army ants based on sample collection time of raids. For species with less than 10 raids I did not classify the activity preference (abbreviation: not class. = not classified).

Species	Day (6am–6 pm)	Night (6pm-6am)	Chi-sq-test	Classification
<i>Eciton burchellii</i>	27	9	$\chi^2=4.8$, $p=0.03$	diurnal
<i>Eciton dulcium</i>	0	11	$\chi^2=7.3$, $p=0.006$	nocturnal
<i>Eciton hamatum</i>	17	4	$\chi^2=4.5$, $p=0.03$	diurnal
<i>Eciton lucanoides</i>	2	2	not applicable	not class.
<i>Eciton mexicanum</i>	1	35	$\chi^2=20.7$, $p<0.001$	nocturnal
<i>Eciton vagans</i>	1	48	$\chi^2=29.3$, $p<0.001$	nocturnal
<i>Neivamyrmex asper</i>	0	2	not applicable	not class.
<i>Neivamyrmex gibbatus</i>	0	20	$\chi^2=13.3$, $p<0.001$	nocturnal
<i>Neivamyrmex pilosus</i>	9	13	$\chi^2=0.4$, $p=0.54$	catheMERal
<i>Nomamyrmex esenbeckii</i>	0	10	$\chi^2=6.7$, $p=0.009$	nocturnal
<i>Nomamyrmex hartigii</i>	0	1	not applicable	not class.

4 Discussion

4.1 Prey Specialization & Networks

In this study, I obtained a thorough sampling of prey for a community of army ants consisting of 11 species. This represents the largest prey assessment of any army ant community study to date. All sampled army ants are specialized predators of ants and prefer immature stages over adults. This shows that they explicitly raid the nest to rob brood and often do not otherwise harm the colonies. If adult ants were among the prey, they were often freshly hatched with soft cuticle. Likely, adult ants are hard to digest because of their strong cuticle, while the soft brood is easily chewable for the army ant larva. Interestingly, pupa cocoons were often removed by army ants during their raids. This has not been described before in literature, and possibly enables easier transportation.

The prey species diversity is very large. So far, around 120 ant prey species could be identified, but as the species accumulation curves imply the actual diversity is expected to be much higher. The amount of prey now already includes roughly 25% of the total ant species richness at La Selva (Longino et al. 2002), which highlights the broad ecological impacts of army ants. Through further barcoding of collected prey items and more sophisticated sampling, this number will very likely increase. Already Rettenmeyer et al. (1983, p.71) stated that “it appears that for every species of ant known in a tropical forest there exists an army ant species [...] to raid it [...]”, which my study seems to confirm.

Within the study area, army ants were very abundant, which is not uncommon in the Neotropics (O'Donnell et al. 2007). It can therefore be expected that their community is shaped by strong interspecific competition. Niche-based specialization processes are thought to be the main drivers of species coexistence, with the general expectation that each sympatric species differs in their resource use (MacArthur 1972; Camarota et al. 2016). Therefore, my main goal in this work was to characterize the specialization of the sympatric community and each army ant species. Specialization is a very broad ecological concept and may include many levels and ecological axis that are highly dependent on the research context (Devictor et al. 2010; Forister et al. 2012). In this work, it is comprehended on a dietary level. There are two possible definitions for a specialist species in regards to its diet which have been analyzed here: a) broadness of food niche (e.g. Shannon diversity of prey species) and b) specialization within the network (i.e. exclusiveness of the use of certain prey within the community). This distinction between individual niche parameters and community-based network analysis can be critical, because the species with the broadest prey spectrum (here *E. lucanoides*) is not necessarily the species with the lowest degree of species specialization in an interaction network (here *E. vagans*).

When analyzing interaction networks one has to acknowledge that the sampling usually represents only a fraction of the actual network (Blüthgen et al. 2006). For instance, rarely collected species often make up a large part of the network, and thus automatically have fewer links; this does not necessarily mean that these species are specialists (Blüthgen 2010). The network specialization index H_2' describes the deviation from a neutral configuration of the network and it is relatively robust by weighting links based on observed interaction

frequencies (Blüthgen et al. 2006; Blüthgen 2010). Thus, even though I was not able to identify a fraction of prey to the species level and did not have sufficient sampling to cover the entire prey spectrum of a species, as indicated by rarefaction curves, the H_2' is likely close to its actual range. Well in accordance with the outlined niche-theory, I found very clear dietary niche differentiation, and despite all army ants being ant specialist on the broad family level, the observed dietary overlap on the lower taxonomic levels was surprisingly small. I found that most army ants have a very high degree of specialization, that varied between values of $d'=0.52$ in *E. vagans* and $d'=0.95$ in *N. pilosus*. This is a much higher specialization than generally found in generalist mutualistic networks (Blüthgen et al. 2007) or plant-herbivore networks (Blüthgen et al. 2006). It comes close to highly specialized networks like parasite-host networks (Esser et al. 2016), which is rather surprising, especially since ants are usually classified as an 'omnivorous' group in ecology (Lach et al. 2010; Rosumek 2017).

In contrast to classical food webs, the interactions within bipartite networks can be quantified and the members of the network have typically a species level resolution (Ings et al. 2009). The taxonomic resolution strongly affects network metrics (Boit et al. 2012). The network here was analyzed in three different taxonomic resolutions (subfamily, genera and species level). Here, I want to explore whether specialization is based on taxonomic preferences, i.e. if one army ant species only takes prey from specific subfamilies of ants. It was observed that with increasing taxonomic resolution the H_2' increased, which is a typical phenomenon since the higher taxonomic level is nested within the lower taxonomic level. The subfamily level resolution was already significantly different from a random network, which means that subfamily prey preference was likely the case but it could not account for most of the observed specialization seen on higher taxonomic resolution.

The obtained diet specialization indices can now be used to study diverse topics, for instance through correlational trait matching. One central question in ecology is the prediction of species abundance, and ecological niche breadth in combination with resource availability seems to be one of the key determinants (Brown 1985). The characterization of the food niche contains valuable information about ecological properties of army ant, such as possible extinction risk which is thought to be higher in specialist species (Devictor et al. 2010; Tylianakis et al. 2010). Specialists are thought to have a lower abundance as their niche breadth

is smaller than that of generalists (Brown 1985), but research on this topic so far has revealed contradicting results (Gregory & Guston 2000; Harcourt et al. 2002; Lawton & Pratchett 2012). An examination of my data did not reveal any correlation between dietary specialization and abundance of army ants, suggesting that the abundance patterns are driven by other factors. Extinction prone are species that specialize on rare resources, but in army ants, even the highly specialized predators like *Neivamyrmex pilosus* consume common and abundant prey, as in this case ants of the genus *Crematogaster*.

Another idea was to find out whether the dietary niche is more similar between closely related species, which would imply that food niche shows long-term stability across taxa during evolution. This is especially pronounced in parasite species (Esser et al. 2016). While obviously a specialization is found on the family of ants (Formicidae), which is likely ancestral in all doryline ants (Borowiec 2016), no such correlation could be found on higher taxonomic resolution, and likely other drivers such as competition lead to differing food niches among closely related species.

4.2 Mechanisms

4.2.1 Spatial niche partitioning

Through characterization of the preys' nesting habits I was able to infer the preferred raiding stratum of the army ant community. I detected clear differences among the army ant species. There were very strict arboreal raiders (e.g. *Ne. pilosus*) and relatively strict ground raiders (e.g. *E. dulcium*) and some species that raided on both strata equally (e.g. *E. lucanoides*). These indirectly inferred specializations were in accordance with direct nest raids I observed in the field, with troops of some species, e.g. *E. vagans* and *E. hamatum*, going up trees more than 20 m and returning with prey.

It is not unsurprising that many army ants also exploit the canopy during their raids. It is estimated that the canopy gives home to more than half of all animal species, and ants can make up more than half of the biomass of all arthropods there (Davidson et al. 2003; Weiser et al. 2010). Canopy ants therefore represent an excellent food resource. While arboreal

raiding has been described as niche partitioning mechanism in Asian *Aenictus* (Hashimoto & Yamane 2014), its role has been largely neglected in Neotropical army ants. Stratum specialization is niche partitioning in space, resulting in less prey overlap of the different species, even if they have a theoretical overlap in their fundamental food niche. For example, *Odontomachus* are frequently raided by *E. vagans* and *E. dulcium*. However, the latter only collects ground living species (most commonly *O. erythrocephalus*), while the former has a wide diversity of more arboreal living *Odontomachus* species (*O. panamensis*, *O. ruginodis*). *Odontomachus erythrocephalus* is also being raided by *E. vagans*, but less commonly so. This results in very few prey overlap on species level resolution. Thus, the spatial differentiation seems to be an important driver of prey specialization.

4.2.2 Temporal niche partitioning

All army ants migrate during the night. This activity is, however, not necessarily linked to raiding activity (O'Donnell et al. 2009). My collection efforts allowed for categorization of species between nocturnal, diurnal and cathemeral raiders. My findings are, for the largest part, in accordance with previous literature description (e.g. Rettenmeyer et al. 1983; Powell & Baker 2008; O'Donnell et al. 2009). An exception is *Nomamyrmex esenbeckii*, which is consistently reported to show diurnal raids (e.g. Powell & Clarke 2004). Perhaps this might be attributed to a higher search time during nighttime compared to daytime resulting in a sampling bias in my results.

Most likely temporal niche specialization cannot explain differences in the prey spectra of army ants, because ant nests of prey species are mostly stationary and do not change their location. Thus, there should be no difference whatsoever in available prey in comparison between day and night (except perhaps for non-ant prey). But temporal niche partitioning among ants has been proposed as mechanism for avoidance of direct resource competition (Anjos et al. 2016; Rosumek 2017) and this is possibly one factor that allows for the high diversity of army ants at La Selva.

4.2.3 Flexibility in prey choice

One important factor known to influence predatory specialization is body size (Dickman 1988; Radloff & Du Toit 2004). While this may indeed play a role, i.e. the tiny *Neivamyrmex* hunt smaller ants than the larger *Eciton* (Rettenmeyer et al. 1983), it is also not a sufficient explanation for most differentiation, e.g. *Eciton* spp. have similar body sizes but still show differences in their prey preferences (see also Powell & Franks 2006). Additionally, colony size and/or polymorphism may play role, i.e. only army ants with sufficient worker force might overwhelm ants with very large, well defended colonies like leaf-cutter ants. Effective defense could also explain why some abundant genera like *Solenopsis* and *Paraponera* are not preyed upon by most army ants. Dejean et al. (2007) documented many anecdotal observations on the defense behavior of ants against army ants, but in some cases the ignorance of certain prey by the army ants is difficult to understand. For instance, *Odontomachus* are not known to exhibit any sort of chemical defense and have rather small colonies. It is thus not intuitively clear why *E. vagans* would readily accept them but *E. burchellii* or *E. hamatum* would not.

Necessary for an explanation is the understanding whether the ants could theoretically prey on certain ants (fundamental niche) but do not prey upon them in the realized niche, possibly due to competition avoidance. Connected to that question is also to what degree the diet specialization is flexible. There has not been much research on this topic. Le Breton et al. (2007) were able to feed specialist *Neivamyrmex* brood from other ants that were not their typical prey under laboratory condition. Furthermore, both Dejean et al. (2007) in Mexico and Rettenmeyer (1963) in Ecuador note a preference of *E. hamatum* for *Camponotus*, which is very different from what was observed in Costa Rica and Panama (Powell 2011). Plasticity in food resource use has been shown in other ants as well, especially in invasive species (Tillberg et al. 2007; Suehiro et al. 2017). Further studies are needed to confirm this, especially since it is possible that *E. hamatum* represents several cryptic species in different regions (e.g. Winston et al. 2016).

In ecology, one should not make the mistake to reduce natural systems to indices and similar parameters. Species identities matters, and therefore I'll provide a rough review about each army ant species I encountered and compare my findings with those of other researchers.

Furthermore, I also provide a short review about army ant species that are not included in this study, as information on their biology in regards to their diet will enhance the narrative scope of this thesis.

4.3 Army Ant Diet

4.3.1 *Neivamyrmex* prey



Fig. 10 *Neivamyrmex gibbatus* raiding a nest of the fungus-grower *Apterostigma collare*.

Neivamyrmex is, after the old-world genus *Aenictus*, the most speciose doryline genus, consisting of around 20 species in Costa Rica alone (Borowiec 2016). I was able to find two species of *Neivamyrmex*, *Ne. gibbatus* and *Ne. pilosus*, on a common basis. Both species are poorly studied. There are some anecdotal descriptions of *Ne. pilosus* prey by Rettenmeyer et al. (1983) who reports that this species raids on *Crematogaster* in Panama. My results for the La Selva community support this description as *Crematogaster* made up a large proportion of *Ne. pilosus* prey. Furthermore, I found that it raids on several species of *Azteca*, which are known for their arboreal habits and close association to *Cecropia* trees (Longino 2007), and on

a small species of *Dolichoderus*. It is noteworthy that all these prey species have arboreal nesting habits.

There is only a short commentary by Rettenmeyer (1963) on *Ne. gibbatus* prey. He just mentions that it consists of ant brood. I found quite diverse ant prey among *Ne. gibbatus* and made several observations on their raiding behavior. They seem to be rather generalist army ants (i.e. have a large prey diversity) and take a diversity of ants from the leaf litter and lower vegetation, such as primitive fungus growers in the genera *Apterostigma* (Fig. 10) and *Cyphomyrmex*, many species of *Pheidole*, *Nylanderia*, *Tapinoma* and also *Aphaenogaster araneoides*.

I was able to find a third species, *Ne. asper*, on two occasions. Since its description by Borgmeier (1955), nothing is known about its biology. Their raids contained brood of *Strumigenys*, *Pheidole* and *Solenopsis*. *Solenopsis* is surprising, because despite having many species and being relative abundant at La Selva (Longino et al. 2002), no other army ant was seen raiding on this genus except *Ne. gibbatus* with very low frequency.

4.3.2 *Nomamyrmex* spp. prey



Fig. 11 *Nomamyrmex esenbeckii* with *Acromyrmex* cf. *volcanus* prey.

Nomamyrmex is a common and widespread genus in Central and South America and forms the sister clade to *Eciton* (Brady et al. 2014). There are two described species in this genus, *No. esenbeckii* and *No. hartigii*, both of which were detected in this study. Little is known about *No. hartigii*; this species seems to have a subterranean lifestyle and is thus hard to find (Borgmeier 1955). According to Rettenmeyer (1963) there are reports that this species preys on termites. I found it only once carrying *Pheidole* brood.

The prey of *No. esenbeckii* is much better known. This species is described as the only army ant capable of raiding the huge colonies of *Atta* leafcutter ants (Swartz 1998; Sánchez-Pena & Mueller 2002; Powell & Clark 2004; Souza & Moura 2008). There are also reports of such raids from La Selva (Longino 2010; Bruce-Sach 2017, pers. comm.), but none of the ten raids I sampled contained *Atta* brood. Instead, *No. esenbeckii* raids often contained *Sericomyrmex amabilis* as prey, another common fungus farming ant with much smaller colony size (Jesovnik & Schultz 2017). In addition, *Pheidole* was found regularly and in one instance also *Acromyrmex*, *Camponotus* and *Pachycondyla*. In two instances I saw the raiding column going

up the trees (*Camponotus* nest: 2 m; *Acromyrmex* nest: >5m; Fig. 11). Arboreal hunting of *N. esenbeckii* on *Camponotus* has been described anecdotally once before, and the authors also recorded raids on *Odontomachus* and termites (Souza & Moura 2008). My results, together with the available literature, suggests that *No. esenbeckii* has a broad prey spectrum, but it seems to raid preferentially on fungus farming ants (especially *Sericomyrmex*).

4.3.3 *Eciton* spp. prey



Fig. 12 Prey cache of *Eciton hamatum* filled with brood of *Pheidole*. Note the myrmecophile staphylinid to the lower right.

Eciton is perhaps the best studied genus of army ants (Borowiec 2016). At La Selva, I found six sympatric *Eciton* species and for all of them I have a decent dataset on their prey spectrum. My results show that they are all specialized ant predators with small food niche overlap.

The most conspicuous species of this genus is *E. burchellii*. Due to their wide distribution range and large swarm raids, this species has received most scientific attention among army ants (Rettenmeyer 1963; Gotwald 1995; Borowiec 2017). Its life history is very well known, and there is a conceivable amount of studies on its prey. For instance, its prey biomass intake has been investigated as well as the identity of many prey items (Franks 1980). My results show that *E. burchellii* is a specialist predator of *Camponotus* ants, which is in accordance with literature observations (Rettenmeyer et al. 1983; Powell & Franks 2006; Powell & Baker 2008). This species is also a generalist predator of various arthropods, which has been more thoroughly investigated than their ant prey. A few records even reported vertebrate prey (Sazima 2017). Kaspari et al. (2011) studied forest floor patches and assessed their arthropod composition before and after raids of the swarm-raiding army ant species *E. burchellii* and *Labidus praedator*. Surprisingly, *E. burchellii* had little to no impact on leaf litter arthropod communities. It was suggested that *E. burchellii* is less effective in searching through the leaf litter, so that a lot of prey escapes. My study suggests an alternative explanation for this result; despite the fact that *E. burchellii* had the largest amount of non-ant prey of all studied species, most of its prey was still other ants (79.4%), primarily arboreal *Camponotus* species. A study by Vieira & Höfer (1994) analyzed the prey spectrum of *E. burchellii* in La Selva, but they focused mostly on spider species and ants were not further identified. They conclude that ants make up 23% (median) of prey in two hours samples. Various explanations could conceivably explain the different proportions of ant prey, for instance different sampling methods or seasonal differences.

Another rather well-known species is *E. hamatum*, a common day active raider. Along its raiding columns they very often build temporary prey caches, which makes the prey collection easy (Fig. 12). Powell (2011) determined the biomass prey intake by *E. hamatum*, which are similar to those reported for *E. burchellii* (Franks 1980). He also identified the most common prey species, *Acromyrmex octospinosus*, which were in 25% of the observed raids and made up 23% of the total prey biomass. Making up 24% of raid samples, my results confirm that *Acromyrmex* is a very common prey item of *E. hamatum*. This was also reported from many anecdotal descriptions (Rettenmeyer et al. 1983). As yet, I was not able to identify *Acromyrmex* prey to species level with high confidence and DNA barcodes did not amplify

consistently (there were only immature stages as prey, no adults). However, it seems likely that most *Acromyrmex* specimens belonged to the species *A. volcanus*, which is the most common arboreal species at La Selva (Wetterer 1993). Further efforts should be taken to reliably identify *Acromyrmex* immatures to the species level and to develop better protocols for amplification of *COI* in *Acromyrmex*.

The remaining species of *Eciton* have a poorly known biology, and all prey reports are anecdotal (Rettenmeyer et al. 1983; Powell & Baker 2008). But there is one notable exception: A sophisticated prey assessment of an *Eciton* community was done by Powell & Franks (2006). They sampled prey of four *Eciton* species on Barro Colorado Island, Panama: *E. burchellii*, *E. hamatum*, *E. dulcium* and *E. mexicanum*. They only assessed the two or three most common genera, lacking any species level identifications. My results match the reported prey preferences for all four species rather well (Table 4). However, few differences were detected. *Pheidole* is lacking as common prey item in Panama, while in my study it is the most common prey for *E. mexicanum* and *E. hamatum*. While *Ectatomma* was also found as prey (~10% of raids), it was by far not the most common prey of *E. mexicanum* (Panama: 68%). Differences in these studies might be attributed to the different sampling location or to different sampling techniques. The study of Powell & Franks (2006) had an evolutionary and functional morphology focus, while my focus was to assess the prey spectrum of army ants in an ecological context.

Tab. 4 Common ant prey genera. Note that our percentages are calculated with relative incidence, while Powell & Franks used relative abundance. Sample size is given as total prey number. *The genera *Mayaponera* and *Neoponera* were known as *Pachycondyla* until revision of Schmidt & Shattuck (2014), and might be included in Powell & Franks' *Pachycondyla*.

Army Ant Species	Powell & Franks 2006	My data
<i>E. burchellii</i>	96% <i>Camponotus</i> n=380	69% <i>Camponotus</i> 10% <i>Pheidole</i> 7% <i>Nylanderia</i> n=467
<i>E. hamatum</i>	23% <i>Acromyrmex</i> n=38 872	39% <i>Pheidole</i> 24% <i>Acromyrmex</i> 16% <i>Trachymyrmex</i> n=530
<i>E. mexicanum</i>	68% <i>Ectatomma</i> 18% <i>Pachycondyla</i> * n=100	20% <i>Pheidole</i> 18% <i>Mayaponera</i> * 12% <i>Pachycondyla</i> * n=436
<i>E. dulcium</i>	53% <i>Odontomachus</i> 47% <i>Pachycondyla</i> * n=450	58% <i>Pachycondyla</i> * 27% <i>Odontomachus</i> 8% <i>Neoponera</i> * n=162

Eciton lucanoides is a rare army ant species, and nothing was previously known on its prey. I found it just five times. It had a surprisingly high diversity of prey species, most notably *Camponotus*, *Trachymyrmex*, *Neoponera*, and also wasps. In contrast, *E. vagans* was the most abundant species in the study area. Its prey habits are very poorly described, e.g. Rettenmeyer et al. (1983) simply stated that they take *Odontomachus* and other ponerines. While there were indeed many *Odontomachus* species among its prey, it also raided on *Pheidole* and *Aphaenogaster* among many others, and often had arboreal raids. *E. vagans* had effectively the lowest degree of network specialization within the community.

4.3.4 Other army ants

4.3.4.1 New World

In this study I collected above-ground raiding army ants. Therefore my collection technique does not accurately represent the whole army ant diversity found at La Selva. There are around 20 army ant species known for this site (Longino 2010), so nearly double the number of species detected in this study. While I covered all *Eciton* and *Nomamyrmex* species, my study did not include many species of the very speciose genus *Neivamyrmex* and I was not able to retrieve prey from *Labidus*. The reason for this might be either because these are very rare or because they have subterranean lifestyle and were not detected with my sampling technique. Therefore, it would be interesting to investigate whether similar prey specialization has been reported from other New World army ant species.

My study covered half of the hitherto described *Eciton* species. There are a total of 12 described *Eciton* species, but two are only known from males (*E. jansoni* & *E. setigaster*) and represent probably other already described species. Additionally, genetic data suggests the existence of several more cryptic species (Winston et al. 2017) so that the taxonomy of this group needs revision. Since most of the Neotropical army ant research was done in Central America, studies on the other species are rare to non-existent (Gotwald 1995). Some anecdotal descriptions from older literature are available, though never going much into detail about army ant prey (Borgmeier 1955).

There is, however, a very good account of the prey from the South American *Eciton rapax* by Kazan (1972). In his master thesis, Kazan (1972) presents a good account of most prey ant species, of which many are even identified to species level. This species also seems to be specialized on ants but takes wasps on occasions. It is reported to prey mostly on ants of the following subfamilies: Ponerinae (genera: *Odontomachus*, *Neoponera*, *Pachycondyla*), Formicinae (genera: *Camponotus*, *Gigantiops*) and Dolichoderinae (genus: *Dolichoderus*). It is interesting to note that this food spectrum differs considerably from the *Eciton* species studied at La Selva; for example, I did not detect an army ant species that raids both on *Odontomachus* and *Camponotus*.

There have been several studies on the prey of *Neivamyrmex* species. Miranda et al. (1980) studied the raiding behavior and quantitatively assessed the prey of the sympatric species *Ne. nigrescens* and *Ne. harrisi* in North America. They found that *Ne. nigrescens* takes primarily species of *Pheidole*, whilst *Ne. harrisi* is a specialist predator of *Solenopsis*. In similar fashion, *Ne. compressinodes* is shown to be specialized on *Wasmannia auropunctata* (Le Breton et al. 2007), and *Ne. rugosus* is a specialized predator of *Trachymyrmex arizonensis* (La Polla et al. 2002). Therefore, all research so far indicates that *Neivamyrmex* is a specialist ant predator (see also Rettenmeyer et al. 1983), and sympatric species diets have little food niche overlap. This is very well in accordance with the community of *Neivamyrmex* studied here.

Labidus consists of seven species of which two are known to occur at La Selva. Both species, *L. praedator* and *L. coecus*, are probably very common, but exhibit a largely underground lifestyle which makes them hard to spot. Because of high colony densities these species probably play an important ecological role, which however remains to be studied in detail (Kaspari & O'Donnell 2003; O'Donnell et al. 2004). Despite their mostly subterranean lifestyle, *L. praedator* are also known to exhibit suspicious above-ground swarm raids similar to those of *E. burchellii* (Borgmeier 1955). Their diet is described to be more generalistic, taking a variety of arthropods but also plant parts (Borgmeier 1955; Viera & Höfer 1994; Monteiro et al. 2008). Kaspari et al. (2011) reported significant reduce in leaf-litter arthropods after a *Labidus praedator* raid passes, and Viera & Höfer (1994) quantified their prey items at La Selva, which contained nearly no ants. There are also reports of *L. praedator* raiding ants of the genera *Camponotus*, *Pheidole* and *Solenopsis* in Paraguay (Fowler 1979), although the degree of specialization in its diet remains poorly quantified. However, it seems clear that they possess a diet niche with much fewer ant prey species than other army ants.

Another South American army-ant is the rarely observed *Cheliomyrmex*. Its presence in Costa Rica is unclear. There are no records from Costa Rica but it was found in Mexico and in Panama. From the few observations made, *Cheliomyrmex* seem to be mostly subterranean. There is an anecdotal report of these ants feeding on a snake cadaver and giant earthworms, suggesting that it might be specialist predator of these (O'Donnell et al. 2005).

4.3.4.2 Old World

Is the observed diet specialization of Neotropical army ants also present in army ants of the Old World? In the following literature account, I will quickly characterize those to give an overview especially in regard to their prey and possible specializations.

The best studied army ant taxon next to *Eciton* is the genus *Dorylus*, which has its main distribution in the Afrotropics, with some species expanding into South-East Asia. Most species are subterranean, but a few species (formerly subgenus *Anomma*; Kronauer et al. 2007) forms large, conspicuous above-ground raids that are known to take a big variety of arthropod prey and even occasionally vertebrates (Gotwald 1995). There are many accounts of the surface raiding *Dorylus*, and all seem to indicate that ants as prey are rather uncommon (Gotwald 1995; Schöning et al 2008). But the other large group of social insects, the termites, are at least for some subterranean *Dorylus* an important prey, although it is unclear whether this is a true specialization as proper quantification is lacking (Berghoff 2003; Schöning & Moffett 2007). Despite the wide food spectrum even in the generalist surface raiders, Schöning et al. (2008) reported different food preferences in two *Dorylus* species: *D. molestus* preyed on a lot of earthworms, whilst *D. wilverthi* did not, which is attributed to different swarm-raiding behaviors (i.e. *D. molestus* shows more digging than *D. wilverthi*).

The genus *Aenictus* is with 183 described species the most speciose genus of all army ants, and somewhat the old-world equivalent to the new world *Neivamyrmex* (Borowiec 2016). They are rather small and monomorphic, and given their hyperdiversity they are vastly understudied. However, there are a lot of observations that indicate that they are ant specialist, and there is even good quantitative data on prey specialization of several sympatric *Aenictus* species: Rościszewski and Maschwitz (1994) studied sympatric *Aenictus* in the Malay Pasoh forest reserve, and concluded that they differed in their food preference based on differences in spatial niche and body size preference. Hirosawa et al. (2000) collected systematically prey items of the same species *A. laeviceps* and *A. gracilis* near Mt. Kinabula, Borneo, and identified them to morphospecies level. They confirmed the suggestion by the earlier study that there is only a very small overlap in prey among both species. Similarly, Hashimoto & Yamane (2014) collected prey items from four sympatric *Aenictus* (two of which

are *A. laeviceps* and *A. gracilis* from the previous studies) on Borneo, Lambir Hills NP. They also found differences in preferred foraging stratum and preferred prey size, resulting in a very small food niche overlap even in those four sympatric *Aenictus*.

While the data on *Dorylus* is too sparse to conclude anything with certainty, the prey specialization of the *Aenictus* community compared to the Neotropical army ants is surprisingly similar. Even the mechanisms (e.g. stratum specialization: see Chapter 4.2.1) seem to be effectively the same. I would therefore predict that any tropical community with army ants around the world will show some niche partitioning with high levels of prey specialization.

5 Conclusions & Outlook

My comprehensive study of army ant prey revealed that all species have a relatively narrow food niche with only little food niche overlap, resulting in highly specialized predator-prey interactions. The degree of diet specialization was neither correlated with army ant phylogeny nor with their abundance.

This specialization is likely the main driver of species co-existence and explains in this context the unusual high diversity of sympatric army ant species, which are among the highest trophic level predators of tropical ecosystems. The mechanisms behind this are not entirely clear, but likely involves niche differentiation on several ecological axes to lower the degree of interspecific competition. For instance, there were clear differences in the stratum use and raiding activity in the community.

In the subsequent literature review, I confirmed many anecdotal descriptions that were made by previous researchers but provided many new observations and reliable quantitative data on the prey of poorly studied species. The observed specialization on ant prey and resulting spatial niche differentiation was also observed in smaller communities of Asian *Aenictus* (Hashimoto & Yamane 2014), and high degrees of specialization on certain ant taxa seems to be common. Likely, this represents a global pattern and I would predict that further studies would find similar differences among army ant communities.

Of high interest would be a comparison between different regions to determine the flexibility of the predator-prey networks. The sympatric community is not the same everywhere and adding or extraction of army ant or prey species might result in different resource use, as was anecdotally observed before (e.g. Rettenmeyer et al. 1983). Of special interest would be the specialization network along a land-use gradient or between primary and secondary forest, as decrease of habitat heterogeneity is thought to increase specialization within predator-prey networks (Staudacher et al. 2018). This would also provide valuable information especially in regards to predator-prey network (re-)assembly mechanisms, which are rather understudied.

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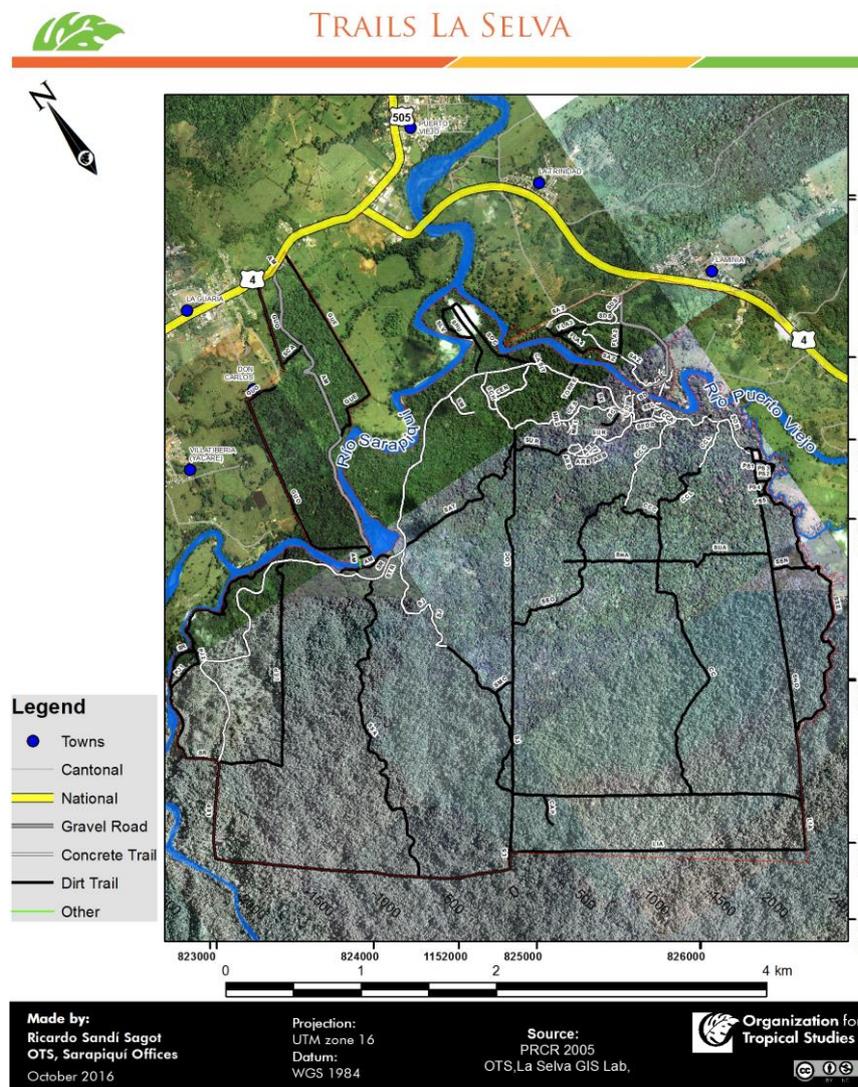
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8 Supplement

Supplement S1: Map of La Selva. All trails within proximity of the station were walked.



Supplement Table S1: List of prey ant species and their nesting stratum. Species not listed were assigned 'Unknown'. The category 'assumed' are species that were not clearly identified on species level but their nesting could be inferred from typical nesting of their genus.

Species	Nesting Types	Source
<i>Acanthognathus ocellatus</i>	both	Longino (2010)
<i>Acromyrmex cf. volcanus</i>	arboreal	Wetterer (1994)

<i>Anochetus mayri</i>	ground	Longino (2010)
<i>Aphaenogaster araneoides</i>	ground	Longino (2010)
<i>Apterostigma collare</i>	arboreal	Longino (2010)
<i>Apterostigma dentigerum</i>	ground	Longino (2010)

Species	Nesting Types	Source
<i>Azteca flavigaster</i>	arboreal	Longino (2010)
<i>Azteca_sp_EC06</i>	arboreal	Assumed
<i>Camponotus brettlesi</i>	arboreal	Longino (2010)
<i>Camponotus excisus</i>	arboreal	Longino (2010)
<i>Camponotus planatus</i>	arboreal	Longino (2010)
<i>Camponotus spp.</i>	arboreal	Assumed
<i>Crematogaster brasiliensis</i>	arboreal	Longino (2010)
<i>Crematogaster carinata</i>	arboreal	Longino (2010)
<i>Crematogaster limata</i>	arboreal	Longino (2010)
<i>Crematogaster_sp_CJ3132-004</i>	arboreal	Assumed
<i>Cyphomyrmex salvini</i>	both	Longino (2010)
<i>Ectatomma gibbum</i>	ground	Longino (2010)
<i>Ectatomma ruidum</i>	ground	Longino (2010)
<i>Ectatomma tuberculatum</i>	ground	Longino (2010)
<i>Gnamptogenys banksi</i>	ground	Lattke 1995
<i>Gnamptogenys haenschi</i>	ground	Longino (2010)
<i>Gnamptogenys mecotyle</i>	ground	Longino (2010)
<i>Gnamptogenys sulcata</i>	arboreal	Longino (2010)
<i>Hypoponera MAS010</i>	ground	Assumed
<i>Mayaponera constricta</i>	ground	Longino (2010)
<i>Megalomyrmex silvestrii</i>	ground	Longino (2010)
<i>Neoponera crenata</i>	arboreal	Longino (2010)
<i>Neoponera apicalis</i>	ground	Longino (2010)
<i>Neoponera bugabensis</i>	arboreal	Longino (2010)
<i>Neoponera lineaticeps</i>	arboreal	Longino (2010)
<i>Neoponera unidentata</i>	arboreal	Longino (2010)
<i>Neoponera villosa</i>	arboreal	Longino (2010)
<i>Odontomachus bauri</i>	arboreal	Longino (2010)
<i>Odontomachus chelifer</i>	ground	Longino (2010)
<i>Odontomachus erythrocephalus</i>	ground	Longino (2010)
<i>Odontomachus hastatus</i>	arboreal	Longino (2010)
<i>Odontomachus meinerti</i>	ground	Longino (2010)
<i>Odontomachus opaciventris</i>	ground	Longino (2010)

<i>Odontomachus panamensis</i>	arboreal	Longino (2010)
<i>Odontomachus ruginodis</i>	arboreal	Longino (2010)
<i>Pachycondyla harpax</i>	ground	Longino (2010)
<i>Paratrechina longicornis</i>	both	Longino (2010)
<i>Pheidole anastasii</i>	arboreal	Longino (2010)
<i>Pheidole boruca</i>	ground	Longino (2010)
<i>Pheidole cf prostrata</i>	arboreal	Longino (2010)
<i>Pheidole cf synarmata</i>	ground	Longino (2010)
<i>Pheidole citrina</i>	ground	Longino (2010)
<i>Pheidole dossena</i>	arboreal	Longino (2010)
<i>Pheidole fimbriata</i>	ground	Longino (2010)
<i>Pheidole fiorii</i>	arboreal	Longino (2010)
<i>Pheidole indagatrix</i>	both	Longino (2010)
<i>Pheidole indagatrix II</i>	both	assumed
<i>Pheidole indagatrix III</i>	both	assumed
<i>Pheidole kukrana</i>	both	Longino (2010)
<i>Pheidole nebulosa</i>	both	Longino (2010)
<i>Pheidole perpusilla</i>	arboreal	Longino (2010)
<i>Pheidole rugiceps</i>	ground	Longino (2010)
<i>Pheidole simonsi</i>	ground	Longino (2010)
<i>Pheidole susannae</i>	both	Longino (2010)
<i>Pheidole vestita</i>	ground	Longino (2010)
<i>Platythyrea cf punctata</i>	arboreal	Longino (2010)
<i>Sericomyrmex amabilis</i>	ground	Longino (2010)
<i>Strumigenys cordovensis</i>	ground	Longino (2010)
<i>Strumigenys elongata</i>	both	Longino (2010)
<i>Strumigenys rogeri</i>	ground	Longino (2010)
<i>Trachymyrmex cornetzi</i>	ground	Longino (2010)
<i>Trachymyrmex intermedius</i>	ground	assumed
<i>Trachymyrmex opulentus</i>	ground	assumed
<i>Trachymyrmex_sp_cornetzi3</i>	ground	assumed
<i>Trachymyrmex_sp_large</i>	ground	assumed
<i>Trachymyrmex_sp_small</i>	ground	assumed
<i>Trachymyrmex_sp1</i>	ground	assumed
<i>Wasmannia auropunctata</i>	both	Longino (2010)

Supplement Table S2: Pairwise H_2' with Patefield Null Modell Method. E.b.= *Eciton burchellii*, E.h.=*Eciton hamatum*, E.l.=*Eciton lucanoides*, E.m.= *Eciton mexicanum*, E.d.=*Eciton dulcium*, E.v.=*Eciton vagans*, Ne.a.=*Neivamyrmex asper*, Ne.g.=*Neivamyrmex gibbatus*, Ne.p.=*Neivamyrmex pilosus*, No.e.=*Nomamyrmex esenbeckii*.

x	E.b.	E.h.	E.l.	E.m.	E.d.	E.v.	Ne.a.	Ne.g.	Ne.p.	No.e.
E.b.	N/A	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
E.h.	<0.001	N/A	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
E.l.	<0.001	<0.001	N/A	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
E.m.	<0.001	<0.001	<0.001	N/A	<0.001	<0.001	0.0149	<0.001	<0.001	<0.001
E.d.	<0.001	<0.001	<0.001	<0.001	N/A	<0.001	<0.001	<0.001	<0.001	<0.001
E.v.	<0.001	<0.001	<0.001	<0.001	<0.001	N/A	0.0899	<0.001	<0.001	<0.001
Ne.a.	<0.001	<0.001	<0.001	0.0115	<0.001	0.0902	N/A	0.3373	<0.001	<0.001
Ne.g.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.3410	N/A	<0.001	<0.001
Ne.p.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	N/A	<0.001
No.e.	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	N/A

Supplement Table S3 Non-Ant Prey

Species	Raid ID	Taxon
<i>Eciton lucanoides</i>	EL34m	wasp larvae
<i>Eciton burchellii</i>	EB30	Wasp, Blattodea
	EB33	Undet.
	EB35	Dermaptera
	EB37	Orthoptera?
	EB42	Blattodea
	EB43	Coleoptera
	EB44	Blattodea
	EB49	Orthoptera
	EB53	Orthoptera
	EB55	Scorpiones
	EB56	Blattodea
	EB58	Wasp
	EB70	Cricket, Cicada
	EB62	Cricket
	EB65	Blattodea
<i>Eciton dulcium</i>	ED41	Chilopoda
<i>Eciton hamatum</i>	EH33	Wasp

Species	Raid ID	Taxon
<i>Eciton hamatum</i>	EH40	Wasp
	EH60	Diptera (Phoridae)
<i>Eciton vagans</i>	EV34	Cricket
	EV47	Diptera
	EV50	Lepidoptera
	EV69	Coleoptera (Cerambycidae)
	EV77	Orthoptera
<i>Eciton mexicanum</i>	EM36	Cicada
	EM49	Hymenoptera
<i>Nomamyrmex hartigii</i>	No10	Cicada

Supplement Observation S4: Intraguild predation in *Neivamyrmex*. During the night (~1 am) of the 06. April 2017 a case of intraguild predation was observed on the CCL trail. *Neivamyrmex* cf. *iridicens* was swarming uncoordinated over a larger area, and their brood was carried around and placed in open brood caches. It looked like a migration, but less coordinated. Another army ant, *Neivamyrmex* cf. *swainsonii*, was observed close the colony. Smaller fights between both species were happening, and *N.* cf. *swainsonii* was seen carrying away brood of *N.* cf. *iridescens*. As this was the only case in which both species were observed, I cannot conclude with certainty if this was an exceptional case or whether there is actually a *Neivamyrmex* species specialized on raiding other *Neivamyrmex*.



Left: *Neivamyrmex* cf. *iridescens* with brood. Right: Fight of *N.* cf. *swainsonii* and *N.* cf. *iridescens*.