

Research Article

Associations of Two Ecologically Significant Social Insect Taxa in the Litter of an Amazonian Rainforest: Is There a Relationship between Ant and Termite Species Richness?

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In spite of the ecological dominance of Neotropical ants and termites, little is understood about how their interactions influence their species richness and distribution. We surveyed ground-dwelling termite and ant species in a primary rainforest in Ecuador and analyzed ecological correlates of diversity. Termite richness was positively correlated with ant richness and abundance of twig-nesting ants. We found no evidence of competition for twigs between termites and ants. No ecological factors were correlated with termite diversity although elevation and twig and log abundance influenced ant diversity. When ant richness was compared to the richness of termites employing different predator defenses, a positive correlation was found with soldierless termites, but not genera employing chemical or mechanical defense. Our results suggest that multiple ecological factors influence ant and termite diversity, and that ant predation on termites may have a greater effect than competition between ant and termites for nest sites and food sources.

1. Introduction

Ants (Order Hymenoptera, Family Formicidae) and termites (Order Isoptera) are among the most prevalent and abundant animals in terrestrial ecosystems [1–3]. Worldwide, 14,550 ant species and subspecies in 283 genera have been described to date [4], and termites are comprised of more than 2866 species in 287 genera [5]. Ants and termites are both entirely eusocial and often form large colonies, contributing to their ecological dominance. In a central Amazonian *terra firme* rainforest in Brazil, ants and termites were found to constitute approximately 75% of soil fauna biomass [6] and 30% of total animal biomass [2]. In this region, Beck [6] estimated that there were 8.6 million ants and 1.3 million termites in a hectare. Ants and termites are most diverse in New and Old World lowland tropical forests, respectively. Termites reach their peak in the Afrotropics, whereas ant diversity is greatest in the Neotropics [7, 8]. Humivorous termites can be exceptionally diverse and abundant in

the Afrotropics [7]. In some areas, termites may constitute up to 95% of the soil insect biomass [9] and local abundance may reach 10,000 termites per square meter [10].

The extraordinary abundance and diversity of ants and termites underscores their importance to tropical terrestrial ecosystems [1, 11–15]. Both ants and termites provide significant ecosystem services, their roles varying in accordance with their very different feeding biology. Termites are decomposers [9] and humivores [16], whereas ants are predators, herbivores, scavengers, and fungivores [17]. In the tropics, leaf-litter and soil-dwelling ants turn over more earth than earthworms [18]. Carnivorous ants are among the dominant predators of invertebrates [1]. In contrast, termites are among the most important decomposers of cellulosic materials. Termites consume as much as 30% of leaf litter in tropical rainforests [19, 20] and can remove 12–57% of available dung in one month [21]. Plant growth tends to be improved on or near termite mounds due to soil modification [22] and higher nutrient content and water availability [23, 24].

Termite food sources—litter, twigs, and decayed wood—are all typical nest sites of ants. Termite feeding may thus potentially limit ant nest site availability and hence diversity. However, ant/termite mutualisms have been reported [1, 25–32], and by sharing nest sites, the presence of termites may increase ant diversity [33]. Dejean et al. [25] found 151 ant species in 725 termitaries and postulated that the availability of suitable nesting sites may impact ant diversity. Termites may also influence ant distribution and diversity because they can represent a significant component of ant diets [34]. Ants in genera such as *Centromyrmex*, *Leptogenys*, *Metapone*, *Ophthalmopone*, *Pachycondyla*, and *Paltothyreus* may feed exclusively on termites [1, 27, 28, 35–38]. While most ant species seem to prey on termites without having a major impact on the survival of established termite colonies [39–41], some ant species may significantly reduce termite populations [37, 42, 43]. Indeed, ant predation is considered to be a major selective force in the evolution of termite defensive strategies [38, 44, 45].

The above-cited studies indicate that Neotropical leaf-litter ants and termites interact primarily as predators and prey and nest mutuals, and termites potentially are indirect competitors with ants for nest sites. The consequences of these interactions could influence ant and/or termite diversity and distribution. Ants have been shown to influence termite abundance, at least in the case of inquilines [46]. Ant and termite diversity in lowland tropical rainforests appears to be especially high [47–49], but there are few comprehensive species inventories. Regional surveys of ants and termites tend to focus on one clade or the other, but rarely both, and their ecological relationships thus remain poorly understood.

Here we report on the results of a survey of the diversity and distribution of ants and termites in the litter layer of a Neotropical rainforest in western Ecuador. Given their varied associations, the relationship between ant and termite diversity and distribution is difficult to predict *a priori*. However, based on the common occurrence of ant predation on termites and potential competition between ants and termites for wood as a nest site or food source, respectively, we hypothesize that (1) the diversity/abundance of twig- and wood-nesting ants will decrease with increasing termite diversity/abundance in the litter due to reduced nest site availability; (2) the diversity of ant genera known to contain termitophagous species will increase with termite diversity; (3) the diversity of ants will increase with the diversity of termites employing antipredatory strategies potentially less efficacious than chemical defense [45, 50–52].

2. Site Description and Sampling Methods

Ants and termites were collected at the Tiptuni Biodiversity Station (TBS) in the western Amazonian rainforest of Ecuador (Orellana Province, 0°37'55''S and 76°08'39''W, altitude 230 m, annual rainfall ~3000 mm), bordering Yasuní National Park. The study site is predominantly primary lowland rainforest with a diverse tree community dominated by the palm *Iriartea deltoidea* [53]. This region of western

Amazonia has been identified as a major tropical wilderness of exceptional richness [54] and holds the global record for regional ant richness [55].

Assessments of the richness of ground-dwelling ants and termites were carried out along three 200 m transects (A, B, and C), with collection points every 10 m. At each sampling point, ants and termites were collected with a pitfall trap (diameter 9 cm, volume 400 mL, collected after 48 hours), a 1 m² Mini-Winkler sample, a bait station (including tuna, peanut butter, cookie, and quinoa collected after 30 minutes), and hand-collecting via careful examination the litter and understory for 15 minutes. The following environmental variables were measured at each of the 60 collection sites (instrumentation/methodology noted in parentheses): microelevation (altimeter), slope (clinometer), canopy cover [56, crown illumination ellipses index], leaf litter depth (average of 10 measurements at each sampling point), bare ground percentage, number of plants/m², number of twigs and logs/m², and volume of twigs and logs/m². Elevation varied only 18 m over our transects (from 206–224 m), though this variation is enough to affect ant diversity [55]. We use the term microelevation because any effects of this variable are likely related to changes in slope and/or water table level rather than climatic variability. A detailed description of the site and methods can be found in Ryder Wilkie et al. [57] and Ryder Wilkie et al. [55]. Means and ranges for all measured environmental variables can also be found in Ryder Wilkie et al. [55]. Ants and termites were collected and identified to species or morphospecies. We noted when ants and termites were found utilizing the same twig or decayed log. Termites were identified at the University of Brasilia, where vouchers have been deposited. Ant vouchers have been deposited in the collection of the Harvard Museum of Comparative Zoology.

To evaluate the potential for competition between ants and termites for twigs in the litter layer, we exhaustively searched leaf litter in 84 three × three meter plots (756 m²) and examined all twigs for nesting ants or feeding termites. We measured the volume of all twigs utilized by each group and rated decay on a scale of 1 (no decay, audible snap when broken) to 5 (highly decayed, crumble at touch) [58]. We also chose one meter at random in each plot and recorded the volume and decay of all twigs within the meter in order to estimate twig availability at TBS. Details of this methodology can be found in Mertl et al. [59]. These data were used to estimate the abundance of ants and termites in twigs but not species richness, as samples of termite species were not collected in these plots.

We define “ground-dwelling” ants and termites as those nesting or active within the litter layer and therefore found using any of the above collection methodologies. Though we have previously collected ants in the canopy and subterranean strata at TBS [55], here we focus only on the litter strata where our methodologies sampled both ants and termites effectively. Our collecting methods were adapted from the ALL protocol, which targets ground-dwelling ants [8]. These methods, which include hand collecting, litter-searching, the use of Winkler devices, and pitfall traps, strongly overlap with those used to sample termites in the litter layer

[60–62]. Our survey does not reflect total termite diversity at TBS, as both canopy and subterranean strata are important to consider when sampling total termite diversity [63].

3. Data Analysis

To assess sampling coverage, species accumulation curves were determined for both ants and termites using EstimateS v 8.2.0 [64]. Multiple regression was used to determine the effects of environmental variation on ground-dwelling ant and termite species richness at the 60 principal sites (20 sites each along transects A, B, and C). At each site, measures of species richness of ground-dwelling ants and termites were based on the incidence of species in pitfall traps, baiting stations, hand collecting, and Winkler samples. Richness was regressed against the eight environmental variables noted previously. An exploratory correlation coefficient matrix of these variables showed that all were at most weakly correlated ($R^2 \leq 0.41$), supporting their independence and allowing for the use of multiple regression (least squares method). Slope, number of twigs and logs, and total volume of twigs and logs were log-transformed prior to regression to improve normality. Canopy cover, percent bare ground, and number of plants could not be normalized through transformation; however, a linear model provided a good fit to the data based on plots showing no correlation between residuals and fitted values ($F < 0.001$, $P > 0.05$ for all regressions) and normally distributed residuals. Separate regressions were run for total species richness of ants and termites. Regression was performed using JMP version 5.0.1 (SAS Institute Inc., Cary, NC, 1989–2002).

To explore competition between ants and termites for wood, we correlated the diversity of twig- and wood-nesting ants and termite diversity based on nesting habits of ants [55], as well as the abundance of twig-nesting ants versus the abundance of twig-foraging termites in the 84 3×3 m plots. We also analyzed the volume and decay distributions of twigs used by twig-nesting ants and twig-foraging termites compared to the available distribution of twigs using ANOVA and Tukey’s HSD with JMP version 5.0.1.

To examine the role of predation and antipredator defenses as determinants of ant and termite species richness, we categorized termite genera according to strategies of soldier defensive behavior (chemical and mechanical defense), separating soldierless termite species in the analysis [44, Table 1]. Although termite soldiers equipped with mandibles to attack predators may possess cephalic glands producing a variety of secretions that could play a role in defense, we classified these species as having mechanical defenses because it is their first line of action and rapid mandibular strike can immediately dispatch an opponent [65]. Nasutitermitinae species, in contrast, rely on terpenoid glues produced by the frontal gland and discharged through the nasus to deter predators [51, 66, 67]. We recognize that soldierless apicotermitine termite species are not defenseless due to their lack of a soldier caste because workers are equipped with a frontal gland and/or paired dehiscence glands that rupture and burst the body wall to discharge defensive compounds

TABLE 1: List of termite species collected at TBS, and their category of soldier defensive strategy.

Termite species	Defense
<i>Anoplotermes</i> sp. 1	Soldierless
<i>Anoplotermes</i> sp. 2	Soldierless
<i>Anoplotermes</i> sp. 3	Soldierless
<i>Anoplotermes</i> sp. 4	Soldierless
<i>Armitermes minutus</i>	Mechanical
<i>Atlantitermes</i> sp.	Chemical
<i>Coptotermes</i> cf. <i>testaceus</i>	Mechanical
<i>Cornicapritermes</i> sp.	Mechanical
<i>Cornitermes</i> sp.	Mechanical
<i>Crepititermes verruculosus</i>	Mechanical
<i>Cylindrotermes</i> cf. <i>nordenskiöldi</i>	Mechanical
<i>Cylindrotermes flangiatus</i>	Mechanical
<i>Cylindrotermes parvignathus</i>	Mechanical
<i>Heterotermes tenuis</i>	Mechanical
<i>Nasutitermes callimorphus</i>	Chemical
<i>Nasutitermes ephratae</i>	Chemical
<i>Nasutitermes guayanae</i>	Chemical
<i>Nasutitermes intermedius</i>	Chemical
<i>Nasutitermes llinquipatensis</i>	Chemical
<i>Nasutitermes longirostratus</i>	Chemical
<i>Nasutitermes</i> sp.	Chemical
<i>Nasutitermes surinamensis</i>	Chemical
<i>Neocapratermes pumilis</i>	Mechanical
<i>Neocapratermes villosus</i>	Mechanical
<i>Rotunditermes braganthinus</i>	Chemical
<i>Ruptitermes</i> sp.	Soldierless
<i>Triangularitermes triangulariceps</i>	Chemical
<i>Velocitermes beebei</i>	Chemical

[68, 69]. We correlated ant diversity with the diversity of termite species in each category of defense. In addition, we examined the species richness of termites in each of the three termite defense categories in samples in which army ants were present or absent using a Mann-Whitney U -test. We also examined the correlation between the species richness of ant genera known to contain a high proportion of termite predators (*Acanthostichus*, *Basicros*, *Centromyrmex*, *Leptogenys*, *Pachycondyla*, *Strumigenys*, and *Tranopelta*) and total termite richness.

4. Results

Twenty-eight termite species in 15 genera (Table 1) and 257 ant species in 56 genera were identified (Table 2, see also [55]). Termites were found at 50 of 60 sample sites (83%). Termites were encountered in 5/60 baiting stations (8.3%), 7/60 pitfall traps (11.7%), 31/60 Winkler (51.7%), and 43/60 hand-collection samples (71.7%). Ants were present in all collections. Species accumulation curves (Figure 1) indicate that additional sampling is required to inventory total species

TABLE 2: List of ant species collected from ground samples at TBS.

<i>Acromyrmex coronatus</i>	<i>Hylomyrma sagax</i>	<i>Pheidole exigua</i>
<i>Acropyga decedens</i>	<i>Hypoponera c.f. creola</i>	<i>Pheidole fimbriata</i>
<i>Acropyga donisthorpei</i>	<i>Hypoponera c.f. distinguenda</i>	<i>Pheidole fracticeps</i>
<i>Acropyga fuhrmanni</i>	<i>Hypoponera c.f. inexorata</i>	<i>Pheidole horribilis</i>
<i>Acropyga guianensis</i>	<i>Hypoponera c.f. parva</i>	<i>Pheidole lemnisca</i>
<i>Amblyopone cf. cleae</i>	<i>Hypoponera perplexa</i>	<i>Pheidole metana</i>
<i>Anochetus diegensis</i>	<i>Hypoponera STD 10</i>	<i>Pheidole midas</i>
<i>Anochetus mayri</i>	<i>Hypoponera STD 11</i>	<i>Pheidole sp. nr. nitella</i>
<i>Apterostigma auriculatum</i>	<i>Hypoponera STD 12</i>	<i>Pheidole peruviana</i>
<i>Apterostigma sp. 2</i>	<i>Hypoponera STD 13</i>	<i>Pheidole pholeops</i>
<i>Apterostigma sp. 3</i>	<i>Hypoponera STD 14</i>	<i>Pheidole sabella</i>
<i>Apterostigma sp. 4</i>	<i>Hypoponera STD 15</i>	<i>Pheidole sagax</i>
<i>Apterostigma sp. 5</i>	<i>Hypoponera STD 16</i>	<i>Pheidole sarpedon</i>
<i>Apterostigma sp. 6</i>	<i>Hypoponera STD 17</i>	<i>Pheidole scalaris</i>
<i>Apterostigma sp. 7</i>	<i>Hypoponera STD 20</i>	<i>Pheidole scolioceps</i>
<i>Azteca SJ-AA</i>	<i>Hypoponera STD 21</i>	<i>Pheidole tobini</i>
<i>Azteca SJ-I</i>	<i>Hypoponera STD 22</i>	<i>Pheidole triplex</i>
<i>Azteca SJ-M</i>	<i>Labidus coecus</i>	<i>Pheidole tristicula</i>
<i>Azteca SJ-P</i>	<i>Labidus punctaticeps</i>	<i>Prionopelta amabilis</i>
<i>Basiceros conjugans</i>	<i>Lachnomyrmex scrobiculatus</i>	<i>Probolomyrmex petiolatus</i>
<i>Basiceros manni</i>	<i>Leptogenys gaigei</i>	<i>Pseudomyrmex tenuis</i>
<i>Basiceros militaris</i>	<i>Leptogenys imperatrix</i>	<i>Pyramica beebei</i>
<i>Brachymyrmex cavernicola</i>	<i>Leptogenys nigricans n. sp.</i>	<i>Pyramica decipula</i>
<i>Brachymyrmex KTRW-001</i>	<i>Leptogenys ritae</i>	<i>Pyramica denticulata</i>
<i>Brachymyrmex KTRW-005</i>	<i>Megalomyrmex balzani</i>	<i>Pyramica depressiceps</i>
<i>Brachymyrmex KTRW-007</i>	<i>Megalomyrmex cuatiara</i>	<i>Pyramica eggersi</i>
<i>Brachymyrmex KTRW-014</i>	<i>Megalomyrmex foreli</i>	<i>Pyramica glenognatha</i>
<i>Brachymyrmex KTRW-015</i>	<i>Megalomyrmex incisus</i>	<i>Pyramica gundlachi</i>
<i>Brachymyrmex KTRW-016</i>	<i>Megalomyrmex mondabora</i>	<i>Pyramica metopia</i>
<i>Camponotus atriceps</i>	<i>Megalomyrmex n. sp. near drifti</i>	<i>Pyramica schulzi</i>
<i>Camponotus claviscapus</i>	<i>Megalomyrmex silvestrii</i>	<i>Pyramica subedentata</i>
<i>Camponotus femoratus</i>	<i>Megalomyrmex timbira</i>	<i>Pyramica urrhobia</i>
<i>Camponotus integellus</i>	<i>Mycetarotes acutus</i>	<i>Pyramica villiersi</i>
<i>Camponotus planatus</i>	<i>Mycetarotes unknown</i>	<i>Pyramica zeteki</i>
<i>Camponotus rapax</i>	<i>Mycocepurus smithii</i>	<i>Rhopalothrix n. sp. 1</i>
<i>Camponotus senex</i>	<i>Myrmelachista KTRW-001</i>	<i>Rogeria blanda</i>
<i>Camponotus WM-009</i>	<i>Myrmelachista KTRW-003</i>	<i>Rogeria ciliosa</i>
<i>Camponotus WM-010</i>	<i>Myrmicocrypta longinoda</i>	<i>Rogeria JSC-001</i>
<i>Carebara angulate</i>	<i>Neivamyrmex pseudops</i>	<i>Rogeria JSC-002</i>
<i>Carebara panamensis</i>	<i>Nomamyrmex esenbecki</i>	<i>Rogeria lirata</i>
<i>Carebara paya</i>	<i>Ochetomyrmex neopolitus</i>	<i>Rogeria micromma</i>
<i>Carebara urichi</i>	<i>Ochetomyrmex semipolitus</i>	<i>Rogeria scobinata</i>
<i>Carebarella KTRW-001</i>	<i>Octostruma iheringi</i>	<i>Rogeria tonduzi</i>
<i>Cephalotes minutus</i>	<i>Octostruma KTRW-002</i>	<i>Rogeria unguispina</i>
<i>Crematogaster carinata</i>	<i>Octostruma KTRW-003</i>	<i>Sericomyrmex sp. 1</i>
<i>Crematogaster erecta</i>	<i>Octostruma KTRW-004</i>	<i>Sericomyrmex sp. 2</i>
<i>Crematogaster flavomicrops</i>	<i>Octostruma KTRW-005</i>	<i>Solenopsis SC-02</i>
<i>Crematogaster levior</i>	<i>Octostruma KTRW-006</i>	<i>Solenopsis SC-03</i>
<i>Crematogaster limata</i>	<i>Octostruma KTRW-007</i>	<i>Solenopsis SC-05</i>
<i>Crematogaster nigropilosa</i>	<i>Octostruma KTRW-008</i>	<i>Solenopsis SC-06</i>

TABLE 2: Continued.

<i>Crematogaster sotobosque</i>	<i>Odontomachus biumbonatus</i>	<i>Solenopsis</i> SC-08
<i>Crematogaster stollii</i>	<i>Odontomachus haematodus</i>	<i>Solenopsis</i> SC-09
<i>Crematogaster tenuicula</i>	<i>Odontomachus meinerti</i>	<i>Solenopsis</i> SC-11
<i>Cyphomyrmex</i> cf. <i>minutus</i> sp. 1	<i>Odontomachus panamensis</i>	<i>Solenopsis</i> SC-12
<i>Cyphomyrmex</i> cf. <i>minutus</i> sp. 2	<i>Odontomachus yucatecus</i>	<i>Solenopsis</i> SC-14
<i>Cyphomyrmex</i> cf. <i>rimosus</i>	<i>Oxyepoecus ephippiatus</i>	<i>Solenopsis</i> SC-16
<i>Cyphomyrmex costatus</i>	<i>Pachycondyla apicalis</i>	<i>Solenopsis</i> SC-17
<i>Cyphomyrmex laevigatus</i>	<i>Pachycondyla arhuaca</i>	<i>Solenopsis</i> <i>virulens</i>
<i>Cyphomyrmex</i> sp. 2	<i>Pachycondyla constricta</i>	<i>Stegomyrmex connectens</i>
<i>Cyphomyrmex</i> sp. 3	<i>Pachycondyla crassinoda</i>	<i>Stegomyrmex manni</i>
<i>Cyphomyrmex vorticis</i>	<i>Pachycondyla gilberti</i>	<i>Strumigenys cosmostela</i>
<i>Discothyrea denticulata</i>	<i>Pachycondyla harpax</i>	<i>Strumigenys elongata</i>
<i>Discothyrea horni</i>	<i>Pachycondyla inversa</i>	<i>Strumigenys perparva</i>
<i>Discothyrea</i> JSC-001	<i>Pachycondyla laevigata</i>	<i>Strumigenys precava</i>
<i>Discothyrea sexarticulata</i>	<i>Pachycondyla lunaris</i>	<i>Strumigenys smithii</i>
<i>Dolichoderus imitator</i>	<i>Pachycondyla verenae</i>	<i>Strumigenys trinidadensis</i>
<i>Dolichoderus rugosus</i>	<i>Paraponera clavata</i>	<i>Strumigenys tridifera</i>
<i>Eciton hamatum</i>	<i>Paratrechina</i> cf. <i>fulva</i>	<i>Tapinoma</i> sp.
<i>Eciton vagans</i>	<i>Paratrechina</i> cf. <i>steinheili</i>	<i>Thaumatomyrmex</i> sp.
<i>Ectatomma edentatum</i>	<i>Paratrechina</i> KTRW001	<i>Trachymyrmex</i> cf. <i>bugnioni</i>
<i>Ectatomma lugens</i>	<i>Paratrechina</i> KTRW003	<i>Trachymyrmex diversus</i>
<i>Ectatomma tuberculatum</i>	<i>Paratrechina</i> KTRW004	<i>Trachymyrmex farinosus</i>
<i>Gigantiops destructor</i>	<i>Paratrechina</i> KTRW005	<i>Trachymyrmex ruthae</i>
<i>Gnamptogenys haenschi</i>	<i>Paratrechina</i> KTRW008	<i>Tranopelta subterranea</i>
<i>Gnamptogenys horni</i>	<i>Pheidole ademonia</i>	<i>Typhlomyrmex pusillus</i>
<i>Gnamptogenys kempfi</i>	<i>Pheidole allarmata</i>	<i>Typhlomyrmex rogenhoferi</i>
<i>Gnamptogenys KTRW-001</i>	<i>Pheidole ALM-006</i>	<i>Wasmannia auropunctata</i>
<i>Gnamptogenys mediatrix</i>	<i>Pheidole ALM-013</i>	<i>Wasmannia</i> cf. <i>lutzi</i>
<i>Gnamptogenys mina</i>	<i>Pheidole ALM-025</i>	<i>Wasmannia scrobifera</i>
<i>Gnamptogenys minuta</i>	<i>Pheidole ALM-026</i>	
<i>Gnamptogenys moelleri</i>	<i>Pheidole ALM-028</i>	
<i>Gnamptogenys pleurodon</i>	<i>Pheidole ALM-031</i>	
<i>Gnamptogenys simulans</i>	<i>Pheidole ALM-032</i>	
<i>Gnamptogenys striatula</i>	<i>Pheidole amazonica</i>	
<i>Gnamptogenys sulcata</i>	<i>Pheidole astur</i>	
<i>Hylomyrma blandiens</i>	<i>Pheidole biconstricta</i>	
<i>Hylomyrma dolichops</i>	<i>Pheidole cephalica</i>	
<i>Hylomyrma immanis</i>	<i>Pheidole cramptoni</i>	
<i>Hylomyrma praepotens</i>	<i>Pheidole deima</i>	

richness of both ants and termites at TBS. Nonparametric estimators ICE, Jackknife1, Jackknife2, and Chao2 (classic) suggest the actual richness of ground-dwelling termites is between 40 and 87 species, and actual ground-dwelling ant richness is between 341 and 383 species. Nine occurrences of termite presence in ant nests were recorded, including termites from four genera (*Cylindrotermes*, *Nasutitermes*, *Rupititermes*, and *Triangularitermes*) found with ants in the genera *Acropyga*, *Gnamptogenys*, *Hylomyrma*, *Hypoconera*, *Pachycondyla*, *Pheidole*, *Strumigenys*, and *Tranopelta* (Table 3).

Ground-dwelling ant species richness increased with microelevation ($t = 5.83$, $P < 0.0001$), as well as the number of logs and twigs/m² in sample plots ($t = 4.70$, $P = 0.035$). The remaining variables were not significant predictors of ant richness across all species, although some variables were significantly correlated in specific genera [55]. A linear multiple regression model showed no significant relationship between the environmental variables measured and termite species richness ($F_{7,52} = 0.80$, $P = 0.614$, adjusted $R^2 = -0.03$).

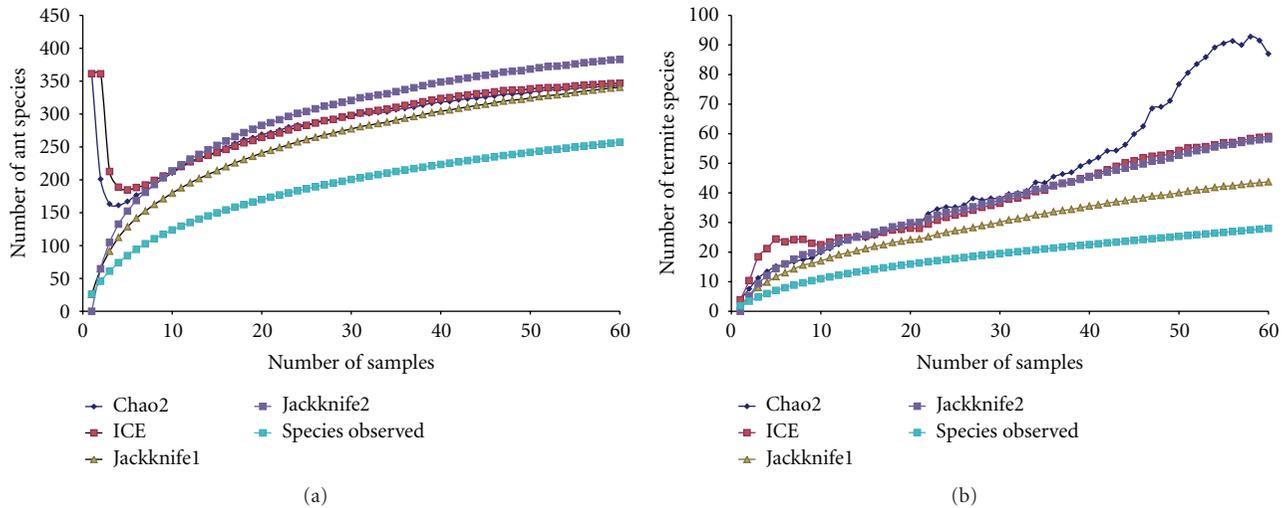


FIGURE 1: Species accumulation curves for (a) ants and (b) termites. Each sample consists of the total species collected via Winkler device, pitfall trap, baiting, and hand collecting at each sampling point ($n = 60$). Values for nonparametric estimators ICE, Jack 1, Jack 2, and Chao 2 (classic) are also shown.

TABLE 3: Ant and termite species collected in the same nest/food source. Termite species were found inside the same twig as the ant species listed next to them, though in separate chambers. Ants and termites were not found to occupy the same galleries within a twig.

Termite	Ant
<i>Cylindrotermes flangiatus</i>	<i>Strumigenys precava</i>
<i>Cylindrotermes parvignathus</i>	<i>Pachycondyla constricta</i>
<i>Nasutitermes ephratae</i>	<i>Gnamptogenys pleurodon</i>
<i>Nasutitermes intermedius</i>	<i>Hylomyrma dolichops</i>
<i>Nasutitermes intermedius</i>	<i>Pheidole amazonica</i>
<i>Nasutitermes llinquipatensis</i>	<i>Tranopelta subterranea</i>
<i>Ruptitermes</i> sp.	<i>Hypoponera c.f. distinguenda</i>
<i>Ruptitermes</i> sp.	<i>Acropyga decedens</i>
<i>Triangularitermes triangulariceps</i>	<i>Pheidole biconstricta</i>

Species richness of termites was positively and significantly correlated with ground-dwelling ant species richness (Figure 2, Spearman's Rho = 0.353, $P = 0.006$, $n = 60$). When the relationship between species richness in ant genera known to include termite predators (*Acanthostichus*, *Basicros*, *Centromyrmex*, *Leptogenys*, *Pachycondyla*, *Strumigenys*, and *Tranopelta*) and termite species richness was analyzed separately, no significant correlation was found (Figure 3, Spearman's Rho = 0.239, $P = 0.068$, $n = 60$). A significant positive correlation was found between termite species richness and the species richness of twig- and log-nesting ants (Figure 3, Spearman's Rho = 0.482, $P = 0.007$, $n = 60$).

There was a significant positive correlation between ant nest abundance and termite forager occurrences in twigs (Spearman's Rho = 0.49, $P < 0.0001$). In respect to the volume of twigs used, ants (mean 108 ± 461 cm³, $n = 342$)

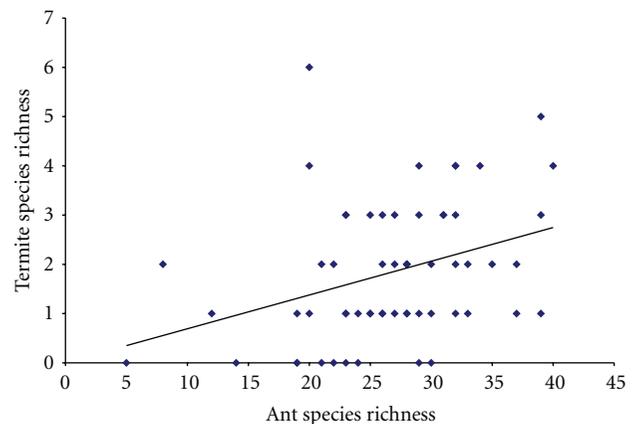


FIGURE 2: Relationship between the species richness of ground-dwelling ants and termites (Spearman's Rho = 0.353, $P = 0.006$, $n = 60$).

showed no difference from the mean available twig size (52 ± 993 cm³, $n = 4509$, Tukey's HSD $P = 0.554$), while termites fed on twigs that were larger than those used for nests by ants (365 ± 915 cm³, $n = 138$, $P = 0.022$) and larger than twigs of average available size ($P = 0.001$). Conversely, mean decay of twigs utilized by termites (3.47 ± 0.852) did not vary from the overall mean decay of twigs (3.57 ± 0.89 , $P = 0.368$), whereas ants nested in twigs that were significantly less decayed than the overall mean decay value (3.35 ± 0.880 , $P < 0.0001$).

When the richness of termites in each of the three termite defense categories was compared between samples in respect to the presence or absence of army ants, no significant differences were found (mechanical: $Z = 0.01$, $P = 0.990$; chemical: $Z = -1.71$, $P = 0.088$; soldierless: $Z = 0.23$, $P = 0.82$). When ant richness was compared to the diversity

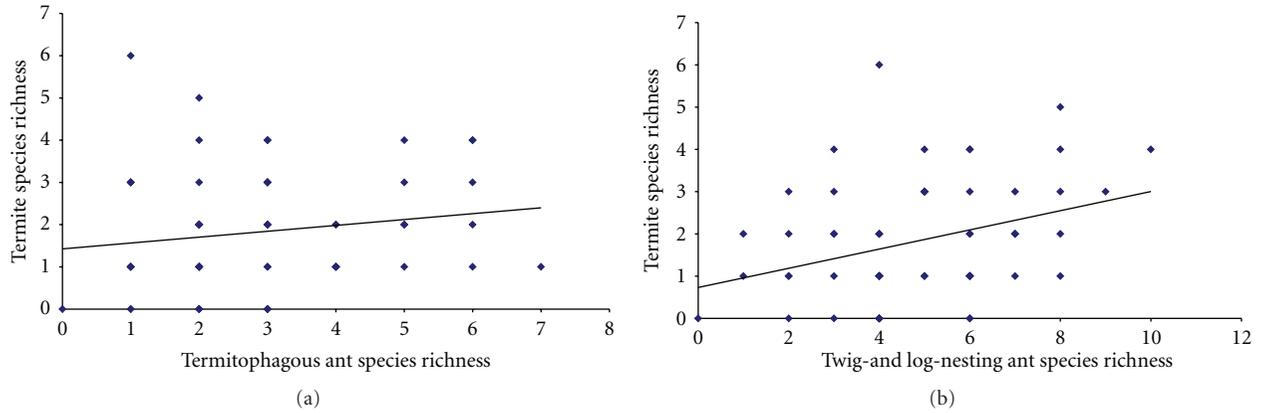


FIGURE 3: Correlation between termite species richness and (a) the species richness of ant genera known to contain termite predators (Spearman's $Rho = 0.239$, $P = 0.068$, $n = 60$) and (b) the species richness of twig and log nesting ant species (Spearman's $Rho = 0.482$, $P = 0.007$, $n = 60$).

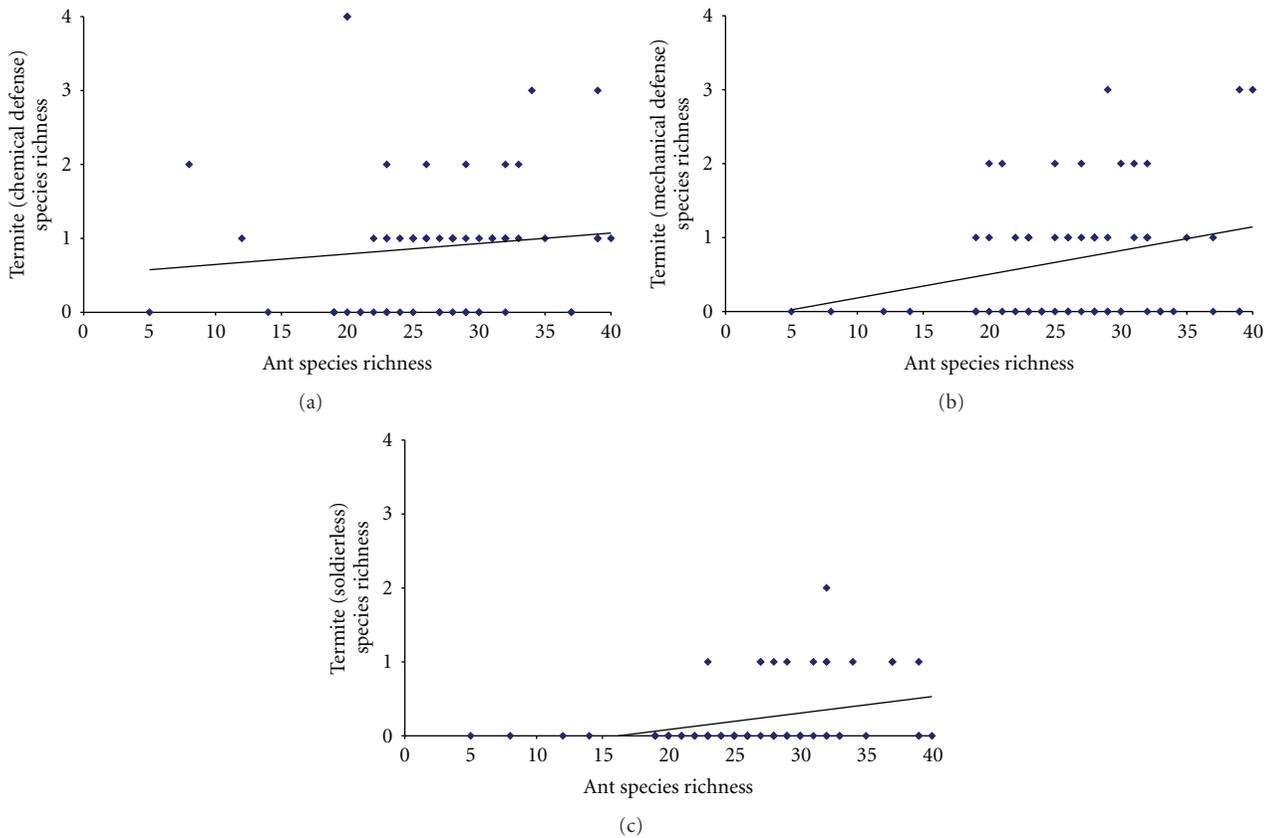


FIGURE 4: Correlation between ant species richness and (a) the species richness of termites with chemical defense (Spearman's $Rho = 0.195$, $P = 0.136$, $n = 60$), (b) the species richness of termites with mechanical (mandibular) defense (Spearman's $Rho = 0.159$, $P = 0.225$, $n = 60$), and (c) the species richness of soldierless termites (*Anoplotermes* and *Ruptitermes*) (Spearman's $Rho = 0.379$, $P = 0.003$, $n = 60$).

of termites employing these different predator defenses, a significant positive correlation was found for the soldierless termite genera *Ruptitermes* and *Anoplotermes* (Figure 4, Spearman's $Rho = 0.379$, $P = 0.003$, $n = 60$), but not for termites with chemical (Figure 4, Spearman's $Rho = 0.195$, $P = 0.136$, $n = 60$) or mechanical (mandibular) defense (Figure 4, Spearman's $Rho = 0.159$, $P = 0.225$, $n = 60$).

5. Discussion

We found 265 ant species and 28 termite species in the litter layer of a lowland tropical rainforest and estimated actual species richness at 346–390 for ground-dwelling ant species and 40–87 for ground-dwelling termite species. Ant species diversity at other Neotropical localities ranges from 74 to 520

species [70–79], while Neotropical termite species diversity, including localities in western Amazonian Brazil, ranges from 26 to 100 species [7, 19, 80–85]. These inventories differ greatly in area surveyed, time frame, collection methods, and goals. Our inventory results fall within the lower end of this range. This is not surprising, because we did not sample subterranean or canopy strata. Accumulation curves indicate that both ant and termite faunas were undersampled [55]. Some of our sampling methods (particularly baiting, in which termites were found in less than 10% of samples) favored the collection of ants. Our Winkler collections as well as hand-collecting and litter-sampling nevertheless yielded termites, including soil-feeding species, in over 50% of samples.

Our results suggest that termite and ant diversity are significantly correlated, perhaps reflecting the nature of their ecological interactions. Termite diversity was not correlated with any of the environmental variables we measured, while ant diversity was correlated with microelevation and the number of twigs and logs in a plot. The positive correlation between termite and ground-dwelling ant species richness suggests that both groups respond similarly to the same, as yet unidentified, environmental factor. We cannot eliminate the possibility that soil humus depth and soil pH [83], clay content and moisture retention [86, 87], dominant tree species [88], total litter weight [89], specific mineral content [87, 90], or other factors influence the diversity and distribution of both groups. However, the relationship between termite and ant diversity may also result from their mutual interactions rather than abiotic preferences and tolerances. Termite distribution can be influenced by intra- and interspecific competition [91, 92], but we are unable to assess the influence of such interactions in our study or separate it from those of ant/termite interaction.

We hypothesized that diversity and abundance of twig- and wood-nesting ants will decrease with termite diversity and abundance, due to the potential for competition with termites for wood resources in the litter. However, we found the opposite pattern: diversity of twig- and wood-nesting ants was positively correlated with termite diversity and the abundance of ants and termites in twigs was also positively correlated. We also found no clear evidence of competition for twigs based on the size or decay of twigs utilized by each group; termites were found foraging in larger twigs than those used for nests by ants, and ants nested in twigs that had less-than-average decay, while termites showed no apparent preference. Termites may select larger twigs for more efficient feeding, while ant species having different body sizes and colony sizes may use a wider variety of nest sizes. Indeed, litter-nesting ants in *terra firme* forest at TBS utilized only 2% of available twigs for nesting, suggesting that competition for nest sites may be negligible [59]. Termite feeding may also be less influenced by decay level than ant presence. Termites and ants may therefore not compete for twig resources.

Contrary to our second hypothesis, the diversity of ant genera known to include termite predators was not significantly correlated with termite diversity. It may be that increased termite diversity does not generate diverse, specific trophic niches for ants, because ants do not appear to

specialize solely on any given termite species. More detailed information on the diets of Neotropical ant species could offer important insights (i.e., [93]). Army ants can be keystone predators in invertebrate communities [94] and army ant raids have been shown to increase with the density of potential prey [95], but we did not find any effect of the presence or absence of army ants on the species richness of termites. The lack of a detectable effect could be due to the nomadic habits of army ants and the relatively sedentary nature of termites and their potentially great abundance. Our results may reflect the importance of opportunistic predation on termites by twig- and wood-nesting species. Predatory ants can negatively influence termite populations [96, 97]. In African grassland, however, overdispersed *Odontotermes* mounds create patches of productivity that positively influence the biomass and fitness of aerial and arboreal arthropods as well as some vertebrates [22]. Predators (spiders and geckos) are more abundant near termite mounds. In our system, predator/prey interactions between ants and termites in the litter may be more significant than competition for wood as a nest site for ants or food source for termites, and ant species density might therefore increase as a function of the diversity and abundance of termite prey species.

Our third hypothesis was supported: we found a positive correlation between ant species richness and soldierless termite genera. However, the association did not hold for termites with chemical or mechanical defense. The autothytic defenses of soldierless termite species may have relatively low efficacy, compared to nasutitermitinae species and other species groups with mobile chemical defenses and secretions that can be repeatedly discharged without loss of soldiers. Chemical defenses are considered to be highly effective in deterring ant predation [98, 99], and *Nasutitermes*, a genus characterized by its prominent terpenoid secretion defenses, is the most species-rich termite genus. Clearly, experimental research is required on the efficacy of termite defenses in the field to fully test this hypothesis.

Our work represents one of the few attempts to survey ants and termites simultaneously and examine how their ecological associations could influence their species richness. As the two most prevalent invertebrates in tropical forests, the dynamics between ants and termites may have strong implications for other invertebrate groups. Ants are symbionts with many species of plants and insects [1, 100]. If the distribution of termites strongly affects ant distributions, termites may also indirectly affect the distribution of mutualistic species. The decomposition and nutrient cycling services provided by termites may also be indirectly controlled by ant predation. Additional studies are needed to better understand mutual influences in these two diverse and abundant groups in the Neotropics as well as how secondary effects of their relationship may impact the functioning of tropical ecosystems.

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