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Community and Ecosystem Ecology

Food Webs in the Litter: Effects of Food and Nest Addition on Ant Communities in Coffee Agroecosystems and Forest

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ABSTRACT Community assembly is driven by multiple factors, including resource availability and habitat requirements. Litter nesting ants respond to food and nest site availability, and adding food and nests may increase ant species richness and abundance. However, litter decomposers share food resources with ants, and increasing food availability may speed decomposition processes, eliminating twigs and seeds in which litter ants nest. We manipulated ant food and nest resources in three habitat types (forest, high-shade coffee, and low-shade coffee) to determine ant community responses after 1 and 2 mo. We examined changes in numbers of ant species, colonies, workers, brood, colony growth rate, and ant species composition. Habitat type strongly affected ant communities, influencing ant species richness, numbers of colonies and workers, and ant species composition. However, food addition and nest addition did not affect these community characteristics. Colony growth rate did not differ with food addition but was greater in forest and low-shade coffee compared with high-shade coffee. Habitat differences in colony growth may be because of presence of an aggressive species (*Wasmannia auropunctata* Roger) in high-shade coffee plots or naturally low arthropod densities during a time when ant colonization was low. Thus, in coffee landscapes, habitat type impacts litter nesting ant community structure, composition, and colony growth rate; however, food and nest addition had small impacts.

KEY WORDS agroecosystem, community assembly, Formicidae, leaf litter, Mexico

Species richness and community composition are mediated by multiple factors (Hunter and Price 1992, Leibold et al. 2004) including differences in food and nesting resources (Hairston et al. 1960, Philpott and Foster 2005, Shik and Kaspari 2010), presence of dominant competitors or predators (Paine 1966), microclimatic conditions (McGlynn et al. 2009), and habitat type (Philpott and Foster 2005, Gibb and Cunningham 2011). In addition, anthropogenic habitat and landscape differences strongly affect biodiversity and community structure (Sala et al. 2000). However, it is still rare for research to combine multiple driving factors within experiments to understand the relative importance of each factor to community organization.

Ants are useful for testing hypotheses about how resources and environmental conditions affect diversity and co-existence (Stanton et al. 2002, Palmer et al. 2003, Sanders et al. 2003, McGlynn 2006), and also act as key indicators of ecosystem processes (Armbrecht and Perfecto 2003). Ants are diverse, and several factors contribute to ant community assembly (Palmer et al. 2003, Andersen 2008). Local influences include microhabitat preferences (Nestel and Dickschen 1990, Kaspari and Weiser 2000, Albrecht and Gotelli 2001, Ribas et al. 2003), lack of preferred size or type of nesting site (Torres and Snelling 1997, Armbrecht et al. 2004), distribution and availability of food (Kaspari et al. 2000, Blüthgen et al. 2004), and interspecific competition (e.g., Parr and Gibb 2010). Leaf-litter nesting ants, in particular, nest in easily manipulated ephemeral resources such as leaf litter and twigs (Kaspari 1996, Armbrecht et al. 2004, McGlynn 2006) and colony growth of litter ants can be quickly assessed by examining changes in the ratio of workers to brood (Kaspari 1996).

Habitat disturbance impacts ant communities (Philpott et al. 2010). Conversion of forest to agriculture results in loss of ant species richness, abundance, and community complexity (Armbrecht and Perfecto 2003, Dunn 2004, Philpott et al. 2008a). Agricultural transformation, including agrochemical use or vegetation changes can affect ants. Coffee agroecosystems, specifically, were traditionally cultivated with diverse, dense shade canopies over coffee plants (Moguel and Toledo 1999), but coffee intensification results in simplification of the shade tree canopy and loss of ant species richness (e.g., Perfecto and Vandermeer 1996). Changes to canopy and understory vegetation results in loss of food resources such as nectar,

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hemipteran honeydew, and arthropod prey. Intensification of coffee farms may also reduce the availability and diversity of nest sites, resulting in nest-site limitation (Armbrecht et al. 2004, Philpott and Foster 2005). Thus, changes in habitat may exacerbate influences of a lack of food and nesting resources that also affect ant communities in forests.

Adding extra protein food resources may have positive or neutral effects on ant communities. With added food, ant colony growth rates may increase (Shik and Kaspari 2010). However, decomposers feed on resources available to ants, thus adding food may accelerate microbial decomposition of litter, limiting the number of nest sites available to ants (Hobbie and Vitousek 2000, Shik and Kaspari 2010). Shik and Kaspari (2010) investigated how adding food and nesting resources affected leaf litter ants in a Panamanian tropical forest and found increases in colony growth and decomposition with added food. In addition, where food and nests were added, colony abundance also increased. We sought to examine whether resource limitation differentially affects ant communities in different habitat types. Specifically, we hypothesized that adding food or nesting resources affects leaf litter ant species richness, colony abundance, and colony growth and that these effects differ in forest and coffee agroecosystems with different shade management. Because coffee farms, and specifically low-shade coffee farms have fewer nesting and food resources than forests, we predicted that adding food and nesting resources would more strongly impact ant communities in coffee agroecosystems compared with forests.

Materials and Methods

Study Sites and Experimental Design. We conducted research in May through July 2010 in Chiapas, Mexico. We established plots in two sites in each of three habitat types near the Finca Irlanda research station (15°11′ N, 92°20′ W): forest, high-shade coffee (or traditional polyculture), and low-shade coffee (or shaded monoculture). All sites were between 800–1,000 m.a.s.l. Replicate sites in the same habitat type were separated by >150 m, a distance larger than the spatial extent of a typical leaf litter ant colony (Agosti and Alonso 2000), and can be considered independent. In each site, we set up four 72 m transects separated by 12 m (Fig. 1). Every 8 m along each transect, we established a 1 by 1 m study plot for a total of 40 plots per site, and 80 study plots in each habitat type. Within transects, we randomly assigned half of plots to food+ and control treatments.

We sampled vegetation in three randomly located 10 by 10 m plots per site. In each plot, we took 15 canopy cover measurements with a convex spherical densiometer. We counted, identified, and measured height and DBH (diameter at breast height) of all trees >5 m tall. We compared vegetation measurements (canopy cover, tree abundance, richness, height, and DBH) with general linear models followed by Tukey's post hoc tests. We adjusted P values with the false discovery rate to account for multiple tests (Benjamini and Hochberg 1995), and report associated P values as P_{FDR}.

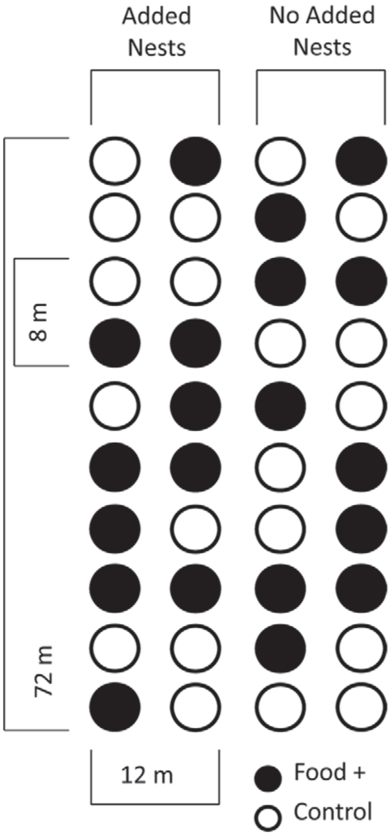

Fig. 1. Experimental design of study plots showing a random distribution of five food+ and five control plots within each transect, and the two transects to which artificial nests were added. Each open or filled circle represents one 1 by 1 m sample plot.

Food Addition. Beginning on 17–21 May, and every 4 d thereafter, we added 5 g of fresh necromass to food+ plots. Necromass consisted of arthropods collected from the study site (primarily Coleoptera, Orthoptera, Diptera, and Diplopoda) and sterile fruit fly pupae (*Anastrepha ludens* Loew) from the Programa Moscafrut in Metapa, Chiapas. We crushed and homogenized all insects before adding them to plots. Necromass has been applied as an ant food source previously (Shik and Kaspari 2010). To ensure ants harvested necromass, we conducted a pilot study. We added 4 g of necromass to note cards on the ground and revisited cards five times in an hour to observe ant activity. Several ant species recruited to and removed necromass. To confirm adding 5 g of necromass was a substantial addition, we collected and dried standing arthropod biomass. For a random selection of 29 control plots (16 forest, nine high-shade coffee, and four low-shade coffee), we extracted arthropods from leaf litter collected for decomposition measurements (see below) in mini-Winkler traps. We dried arthropods for 24 h at 60°C, weighed arthropods and compared this value to 5 g of dried necromass with a general linear model.

Ant Sampling and Community Analysis. We collected ants in randomly selected plots (half of food+ and control plots) 1 (17–21 June) and 2 mo (12–16 July) after beginning food addition to examine impacts on ant communities. We inspected leaf litter and natural nest cavities (e.g., seedpods, twigs, and rotten logs) in the 1 by 1 m plot and collected all ant colonies. We placed each colony into a bag, and later transferred ant colonies into vials with 75% ethyl alcohol. We identified all ants to species or morphospecies. We deposited voucher specimens at the University of California, Santa Cruz.

We compared the numbers of ant colonies, species, brood, and workers according to habitat, food treatment, and month with generalized linear models with a Poisson regression assuming a log-link function because the data did not conform to the assumptions of normality and because we analyzed count data. To correct for over dispersion, we adjusted models using a scaling parameter in the GENLIN function of SPSS 16.0 (inverse of the Pearson χ^2 value/df) (McCullagh and Nelder 1989, Wilson et al. 1996). We included all two- and three-way interactions in the model. We also included leaf litter depth as a covariate, but this had no influence on the results, so we report results without inclusion of leaf litter depth here. We calculated Wald χ^2 statistics type III sum of squares. We compared habitat pairs using estimated marginal means with Bonferroni corrections and designate corresponding P values as P_B. We compared ant species composition among habitats and food treatments with nonmetric multidimensional scaling (NMDS) and analysis of similarities (ANOSIM) with the Bray–Curtis similarity index with PAST (Hämmer et al. 2001).

Ant Colony Growth. We compared differences in colony growth with habitat and food treatment with analysis of covariance (ANCOVA). We used number of brood in a colony as the dependent variable, the number of workers as a covariate, and food treatment and habitat as independent factors. We first tested the null hypothesis that the slope of the relationship between workers and brood differed by food addition treatment or by habitat type. If we did not reject the null hypothesis (e.g., similarity in slopes assumed), we examined for differences in brood number with food treatment or habitat. We completed analyses for all colonies together and for common species found from >10 colonies. We used log transformed count data (ln + 1) for both workers and brood.

Natural and Artificial Nests. We counted the number of natural nests (e.g., seedpods, twigs, and rotten logs) encountered during ant surveys. To detect if ant nest-site limitation was affected by food addition, we added artificial nests at the onset of the experiment (17–21 May). Artificial nests consisted of hollow bamboo sticks 10–15 cm long and 5–10 mm diameter. These artificial nests are colonized by several species, and sometimes after only 2 wk (Philpott and Foster 2005, Shik and Kaspari 2010). Nests were tied to stakes, and four nests per plot were placed horizontally on the ground in two transects per site (10 food+ and 10 control plots) (Fig. 1). We collected nests 1 or 2 mo later (in plots randomly selected for ant sampling) and identified ant occupants. We counted all workers, queens, and brood. We compared the number of natural nests and proportion of occupied artificial nests with general linear models with habitat type, food treatment, and month as main factors, and compared habitat pairs with Tukey's tests.

Decomposition. We examined the impacts of habitat and food addition on litter decomposition in three ways. First, we noted mass lost from course filter paper (100% cellulose, Fisher 09–975C) across the 2-mo sample period. We weighed filter papers, placed them into mesh bags (hole size 1 by 1 mm), and placed two bags in each 1 by 1 m plot. We collected half of bags after 1 mo, and the other half after 2 mo. We then removed remaining paper from bags, dried paper at 60°C for 48 h, reweighed samples, and calculated mass lost. Second, we measured leaf litter depth at the start of the experiment and when ants were sampled (at 1 and 2 mo). We inserted a marked wooden rod through the litter to the soil surface at four corners of plots. Third, we collected all litter from plots after sampling for ants, and dried litter at 60°C until no additional mass was lost with additional drying. We compared proportion of filter paper mass lost (Arcsine square root transformed), change in litter depth, and dry litter biomass (ln) among habitats, food treatment, and month with general linear models, and compared habitat pairs with Tukey's tests. Unless otherwise noted, all statistical tests were conducted with SPSS 17.0.

Results

Vegetation. Some vegetation characteristics differed with habitat type. Canopy cover, tree abundance, and tree richness were higher in the forest than in coffee habitats, canopy cover was higher in high-shade coffee than in low-shade coffee, but tree height and DBH did not differ with habitat type (Table 1).

Arthropod Biomass. Necromass addition increased arthropod biomass by two orders of magnitude ($F_{3,30} = 48.203$; $P < 0.001$). When dried, 5 g of necromass weighed 1,640 ± 80 mg, and dry arthropod biomass was 17.31 ± 6.35 mg in forest, 3.67 ± 0.74 mg in high-shade and 16.75 ± 7.4 mg in low-shade coffee. Standing biomass differed with habitat type ($P < 0.001$ per pair-wise comparison).

Ant Community. Poisson regression analysis shows that habitat affected ant communities, but food addition did not, and there were no significant interactions between habitat and food addition. We collected 184 ant colonies; 80 from forests, 65 from high-shade coffee, and 39 from low-shade coffee. The number of ant colonies differed with habitat and month, but not with food addition (Table 2; Fig. 2a). There were twice as many colonies in forests than in low-shade coffee ($P_B = 0.001$), and 59% more colonies in high- than in low-shade coffee ($P_B = 0.053$), but no differences between forest and high-shade coffee ($P_B = 0.53$). We

Table 1. Vegetation differences in forest, high-shade, and low-shade sites sampled for ants in Chiapas, Mexico

	Forest	High-shade coffee	Low-shade coffee	$F_{2,3}$	P^b
Canopy cover (%)	87.78 ± 4.17a[a]	68.89 ± 5.83a,b	36.8 ± 5.41c	24.707	0.023
No. tree individuals	16.17 ± 0.5a	4.5 ± 1.17b	1.67 ± 0.33b	102.887	0.005
No. tree species	10 ± 1a	3.5 ± 0.83b	1.33 ± 0.33b	33.8	0.045
Tree ht (m)	8.49 ± 1.24	14.36 ± 2.84	5.52 ± 3.73	2.581	0.223
Tree DBH (cm)	14.00 ± 2.69	30.59 ± 1.61	13.30 ± 8.89	3.227	0.223

[a] Numbers show mean ± SE for each habitat type. Small letters indicate significant pairwise differences between habitat types as indicated by Tukey's post hoc tests.

[b] P values are adjusted for multiple tests with the false discovery rate (see text for explanation).

found 36 morphospecies of ants; 28 in forests, 22 in high-shade coffee, and 19 in low-shade coffee (Supp. Table 1 [online only]). Ant species richness differed with habitat type, but not with food addition (Table 2; Fig. 2b). Ant species richness was twice as high in forests than in low-shade coffee ($P_B = 0.002$), but did not differ among forest and high-shade coffee ($P_B = 0.174$) or between high- and low-shade coffee ($P_B = 0.32$). There were four times more brood in the forest ($P_B = 0.037$) and in high-shade coffee ($P_B = 0.018$) than in low-shade coffee (Table 2; Fig. 2c), but brood did not differ in coffee habitats ($P_B = 1$). Worker numbers differed with habitat, but not with food addition or month (Table 2; Fig. 2d). The number of workers was more than twice as high in high-shade coffee than in low-shade coffee ($P_B < 0.001$) but did not differ between forest and high- ($P_B = 0.130$) or low-shade coffee ($P_B = 0.138$).

Ant species composition differed with habitat (Global $R = 0.02$; $P < 0.001$), but did not differ with food addition (Global $R = 0.009$; $P = 0.851$; Fig. 3). Forest ants differed from high-shade coffee ants ($P = 0.004$) and from low-shade coffee ants ($P = 0.028$). High- and low-shade coffee ants did not significantly differ ($P = 0.094$).

Colony Growth. There were no differences in colony growth with food addition in any habitat but colony growth differed with habitat type (Fig. 4). Brood and worker numbers were positively correlated ($F_{1,174} = 258.057$, $P < 0.001$; control, $y = 0.9094x + 0.2763$, $R^2 = 0.5812$; food+, $y = 0.9633x + 0.2613$, $R^2 = 0.6418$; forest, $y = 1.0414x + 0.1164$, $R^2 = 0.646$; high-shade coffee, $y = 0.9705x - 0.2341$, $R^2 = 0.5922$; and low-shade coffee, $y = 0.8993x + 0.5778$, $R^2 = 0.6572$). The slope of the brood to worker relationship, however, did not differ with habitat type ($F_{1,174} = 0.018$; $P = 0.895$) or food addition ($F_{1,174} = 0.454$; $P = 0.636$). Further, brood number did not differ in food+ and control plots, after accounting for differences in worker numbers ($F_{1,177} = 1.082$; $P = 0.30$), nor did food addition effects differ with habitat type ($F_{2,177} = 0.078$; $P = 0.943$). However, brood numbers (after accounting for differences in numbers of workers) did differ with habitat ($F_{2,177} = 5.499$; $P = 0.005$). There were more brood per worker in forests ($P = 0.009$) and low-shade coffee ($P = 0.026$) than in high-shade coffee, but no difference between forest and low-shade coffee ($P = 1.00$). Food addition did not affect colony growth of three of four of the most common species. For *Solenopsis* sp. 1, there was a significant interaction between worker numbers and food treatment (ANCOVA; $F_{1,27} = 2.664$; $P = 0.007$); thus, we did not examine effects of food addition. The number of *Brachymyrmex* sp. 1 brood ($F_{1,10} = 0.223$; $P = 0.647$), and *Solenopsis zeteki* Wheeler brood ($F_{1,13} = 0.035$; $P = 0.855$) per worker were similar in the food+ and control plots. However, there were more *Wasmannia auropunctata* Roger brood per worker in food+ compared with control plots ($F_{1,17} = 4.266$; $P = 0.054$).

Natural and Artificial Nests. We found 6.38 natural nests (e.g., twigs and seeds in leaf litter) per plot. Natural nest numbers were similar in food+ (6.21 ± 0.1.76 (SE)) and control plots (6.55 ± 1.24) ($F_{1,12} = 2.548$; $P = 0.136$). We found twice as many natural nests in the forest (11.56 ± 1.94), than in high-shade coffee (4.89 ± 0.61), and fewest in low-shade coffee (2.70 ± 0.85) ($F_{2,12} = 65.64$, $P < 0.001$; $P < 0.001$ for pairwise comparisons). We recovered twice as many nests after 1 mo (8.73 ± 1.70) than after 2 mo (4.04 ± 0.87) ($F_{1,12} = 54.63$; $P < 0.001$). There were no significant interactions between food addition, month, and habitat. We recovered 398 of 480 artificial nests,

Table 2. Results of a Poisson regression analysis testing effects of habitat, month, and food addition on species richness, colonies, and workers in forests and coffee farms

Source	Richness		Colonies		Brood		Workers	
	χ^2	P	χ^2	P	χ^2	P	χ^2	P
Intercept	30	<0.001	18	<0.001	427	<0.001	385	<0.001
Habitat	12	0.003	13	0.002	7.0	0.03	13	0.001
Month	3.8	0.050	4.3	0.038	1.1	0.304	0.0	0.942
Food	2.1	0.148	2.6	0.106	0.0	0.876	0.9	0.353
Habitat × month	0.4	0.837	0.2	0.923	1.0	0.606	0.2	0.913
Habitat × food	0.9	0.623	1.6	0.460	0.2	0.909	0.7	0.69
Month × food	0.0	0.868	0.1	0.819	0.1	0.769	0.1	0.723
Habitat × month × food	0.0	0.538	1.1	0.565	0.9	0.630	0.6	0.757

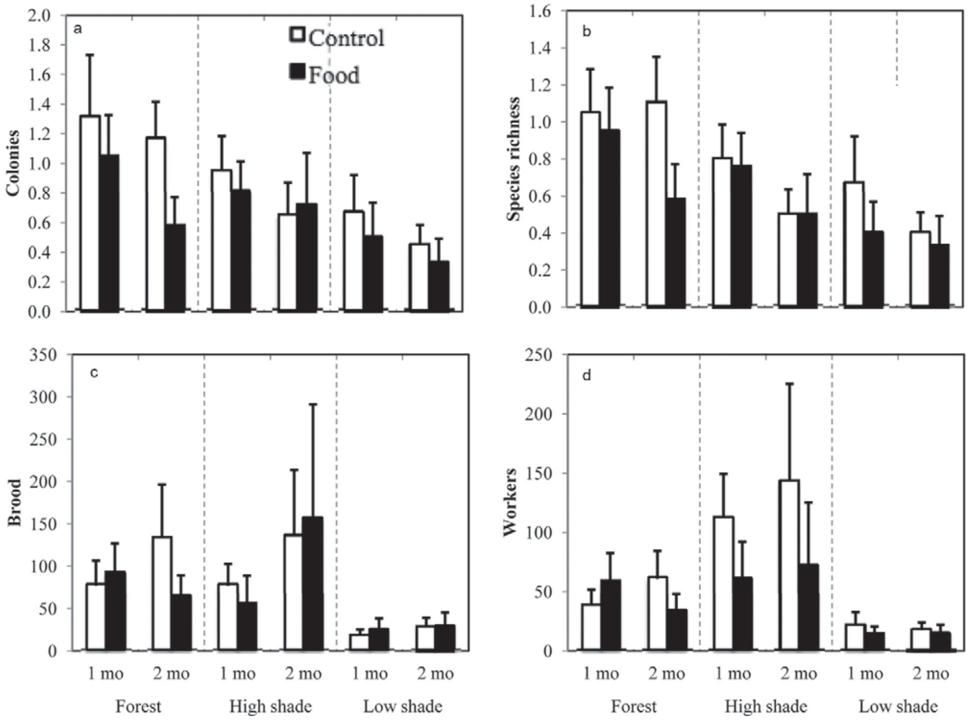

Fig. 2. Mean (±SE) number of (a) colonies, (b) species, (c) brood, and (d) workers per plot across habitat type, sampling month, and food addition treatment.

198 from food+ plots and 200 from control plots. Ants only occupied 5 artificial nests; 4 in control plots (1.96% of nests placed), and 1 in a food+ plot (0.49%). Ants occupied 2.14% of nests in high-shade coffee, 1.31% of nests in low-shade coffee, and 0% of nests in the forest. Ants occupied 1.27% of nests collected after 1 mo, and 1.16% of nests collected after 2 mo. Because of low numbers of occupied nests, we did not statistically analyze artificial nest data.

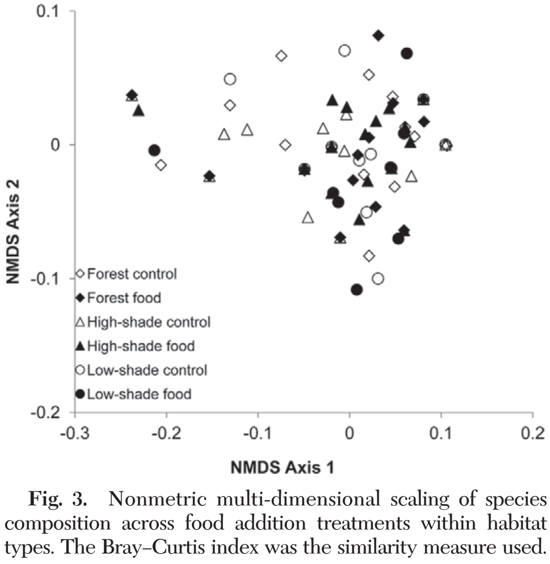

Fig. 3. Nonmetric multi-dimensional scaling of species composition across food addition treatments within habitat types. The Bray–Curtis index was the similarity measure used.

Decomposition. Leaf litter decomposition differed with habitat, and increased over time, but did not differ with food addition. Filter papers decomposed half as quickly in low- than in high-shade coffee ($P = 0.01$) or in the forest ($P = 0.001$) ($F_{2,12} = 13.564$; $P = 0.001$) (Table 3). Filter papers lost twice as much biomass after 2 mo than after 1 mo ($F_{1,12} = 25.302$; $P < 0.001$). Food addition did not affect mass lost from filter papers ($F_{1,12} = 0.055$; $P = 0.819$). Changes in leaf litter depth did not differ with food addition, but reduction in litter depth differed with habitat and month (Table 3). Reduction in litter depth did not differ with food addition ($F_{1,\ 12} = 0.417$; $P = 0.531$). Twice as much litter depth was lost in the high-shade coffee than in forest ($P = 0.08$) or in low-shade coffee ($P = 0.065$); litter depth loss was similar in forest and low-shade coffee ($P = 0.992$) ($F_{2,12} = 4.035$; $P = 0.046$). Litter depth loss did not differ between 1 and 2 mo ($F_{1,12} = 2.157$; $P = 0.168$). Finally, leaf litter biomass did not differ with food addition ($F_{1,11} = 0.41$; $P = 0.535$) or habitat ($F_{2,11} = 1.281$; $P = 0.316$), but litter weighed less after 2 mo ($F_{1,11} = 18.562$; $P = 0.001$; Table 3). There were no interactions between food treatment, habitat type, or month for any variable.

Discussion

In our experiment, food addition did not affect ant communities in forests, high-shade coffee, or low-shade coffee habitats. There was no effect of food addition on ant species richness, numbers of colonies,

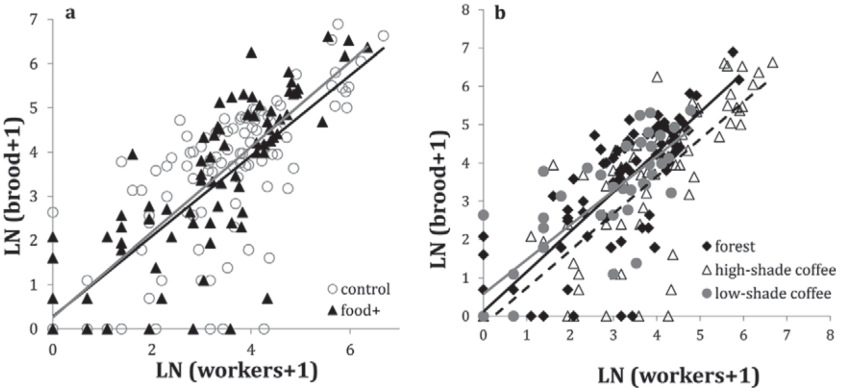

Fig. 4. Differences in ant colony growth rates measured by worker to brood ratio. Panels show comparisons based on (a) food addition treatment and (b) habitat type. Each point represents a colony. Food addition did not alter worker:brood ratios; however, forest and low-shade coffee plots had higher numbers of brood after accounting for differences in worker number (see text for explanation).

brood, or workers, or on ant species composition. Moreover, food addition did not affect litter decomposition or the number of available nest sites. These results are consistent with other studies that failed to find evidence that food alone is a limiting resource for ant colonies (Aron et al. 2001, McGlynn 2010, Shik and Kaspari 2010). However, colony growth sometimes increases with food addition (e.g., Deslippe and Savolainen 1994, Aron et al. 2001, Brown and Keller 2006, Fokuhl et al. 2007). Of the two studies that have added food for tropical litter ants, one found an increase in ant density (McGlynn 2006), and the other found increases in ant densities when nest sites were also added (Shik and Kaspari 2010).

Food addition may have had limited effects in our study for several reasons. First, arthropod abundance is generally higher in the tropical wet season (Levings and Windsor 1985), the time our study was conducted. Second, our experiment may have been too short to detect increases in colony density or colony growth rates. Nevertheless, others have found changes in colony density in extremely short time scales. McGlynn (2006) observed large changes in nest density after 3 mo of food addition; but in this same study explained that litter ants may move their nests in the space of a few weeks. Other litter ant studies document that ants move monthly (Kaspari 1996). Shik and Kaspari's (2010) experiment ran for 2 mo with an additional experiment for 1 mo and they observed effects of food addition after 2 mo, and nest addition effects after 2 wk. Indeed many ants display an 'unstable nesting' syndrome in which they nest in ephemeral resources, like folded leaves or decaying plant material, that then requires movement on a short term basis (McGlynn 2012). For example, Smallwood (1988) found that three of five ant species moved nests on average after less than a month in West Virginia. Similarly, 43% of Argentine ant nests move within the first month (Heller and Gordon 2006). Thus, our experimental duration of 2 mo might be considered somewhat short, but should have been long enough to capture ant colonies relocated to capture resources within plots. Third, some queens are inflexible in adjusting brood rearing as food availability changes (Pacheco et al. 2009). Regardless, many litter ant nests are ephemeral (Shik and Kaspari 2010); thus, much movement is because of nest relocation rather than colony founding (McGlynn 2006). Finally, we found a low number

Table 3. Decomposition measures in forests and two coffee agroecosystems differing in shade management and with (food+) and without (control) necromass addition

	1 mo		2 mo	
	Control	Food+	Control	Food+
Disk weight lost (%)				
Forest	0.57 ± 0.04	0.64 ± 0.08	0.74 ± 0.13	0.73 ± 0.03
High-shade coffee	0.41 ± 0.07	0.38 ± 0.09	0.74 ± 0.07	0.75 ± 0.04
Low-shade coffee	0.22 ± 0.09	0.22 ± 0.09	0.47 ± 0.1	0.52 ± 0.12
Litter depth lost (cm)				
Forest	0.76 ± 0.18	0.95 ± 0.34	1.56 ± 0.36	2.33 ± 0.39
High-shade coffee	1.92 ± 1.49	2.88 ± 0.88	2.75 ± 0.43	2.92 ± 0.39
Low-shade coffee	1.13 ± 0.34	1.25 ± 1.09	1.79 ± 0.96	1.19 ± 0.44
Litter mass (g)				
Forest	246.28 ± 92.6	411.99 ± 32.61	231.14 ± 22.89	196.7 ± 43.32
High-shade coffee	285.1 ± 23.98	304.37 ± 22.33	114.2 ± 57.24	170.94 ± 17.79
Low-shade coffee	563.25 ± 187.58	434.59 ± 206.53	163.5 ± 65.17	161.52 ± 9.67

See text for statistical results.

of ant colonies relative to other litter ant studies conducted in lowland tropical forests, and little variation in abundance and richness in our study sites may have limited our power to observe treatment differences.

We did not find any evidence here that leaf litter ants are nest-site limited. This is in contrast to other studies in both forest and coffee agroecosystems. Shik and Kaspari (2010) found high nest occupation in food+ plots and reasoned that decomposition of ephemeral nest resources in food+ plots may limit ants where food is abundant. Others have documented limited colonization in areas with accelerated decomposition, food addition, or manual removal of leaf litter (Kaspari 1996, McGlynn 2006, Kaspari et al. 2009). Kaspari et al. (2009) noted that ants are more likely nest limited in areas with strong bottom-up forces and that ants are better at colonizing areas where top-down forces are more influential. In addition, Armbrecht et al. (2004) documented high occupation of artificial litter nests in coffee farms in Colombia. As a side note, we did observe differences in litter weight 1 and 2 mo after food addition began. This is likely because of lower litter fall and greater decomposition during the tropical wet season that began at the start of our study (Wieder and Wright 1995). However, changes in litter depth did not correspond to changes in colony size in our study.

We did encounter differences in richness, numbers of colonies, and species composition among habitat types. Ant species composition differed among forests and the two coffee habitat types. Differences in colony size between habitat types could result from differences in species composition or because of differences in nest availability, food availability and distribution, and microclimate may affect ants (e.g., Kaspari 1996, McGlynn 2006) and many of these factors differed between habitats. Standing biomass of arthropods, number (and likely diversity) of twigs was highest in forests. Food availability, even if not limiting, affects colony growth and colony abundance, and higher arthropod biomass in the forest and low-shade coffee may have contributed to greater colony growth rates therein. If food was significantly limiting in the high-shade coffee, some ants may have cannibalized workers and brood to maintain colonies (Pacheco et al. 2009) resulting in apparent low colony growth rates. Increases in the number and diversity of litter twigs positively affect leaf litter ants (Armbrecht et al. 2004). We found more natural nests in forests than in the high- or low-shade coffee, and this may have influenced the numbers of species and colonies. Findings of lower colony density and ant species richness in more intensively managed coffee farms are consistent with other agricultural studies. Ant diversity and density is often similar in forests and shaded agroforests (e.g., Belshaw and Bolton 1993, Philpott et al. 2008a) but litter ant species richness and density decline in progressively more intensive coffee farms (Armbrecht et al. 2005). In temperate agricultural systems, litter ant species richness is greater in less intensive farms (Peck et al. 1998).

Colony growth rates of most common ant species were not affected by food addition; however, *W. auropunctata* colony growth was higher with food addition. This species only occurred in the high-shade coffee, the habitat with significantly lower colony growth overall. *W. auropunctata* is an aggressive ant that impacts ant communities outside of its native range (Le Breton et al. 2003). Colony growth in each habitat was examined both with and without *W. auropunctata* colonies; the qualitative result was the same. Even with *W. auropunctata* data points removed, habitat type remained an important factor for colony growth rate ($F_{2,160} = 4.853$; $P = 0.009$). Although several mechanisms might explain how *W. auropunctata* may have limited growth of other ant species within the high-shade coffee, one recent study points to a potential mechanism whereby *W. auropunctata* invade nests of other species and consume their workers and brood (Vonshak et al. 2012). Thus, *W. auropunctata* may have preyed on individuals of other species, leading to increased colony growth after other ants harvested added food.

In summary, we found no differences with food addition and no significant interaction in the effect of food addition in different habitat types. Thus, food availability in coffee agroecosystems and adjacent forest fragments does not appear to limit ant communities, nor does the degree to which food limits ant communities here appear to differ with habitat type, however, changes in growth rates of certain aggressive species may alter interactions between ant species and may change when food resources are added.

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