More food, less habitat: how necromass and leaf litter decomposition combine to regulate a litter ant community

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Abstract. 1. In brown food webs of the forest floor, necromass (e.g. insect carcasses and frass) falling from the canopy feeds both microbes and ants, with the former decomposing the homes of the latter. In a tropical litter ant community, we added necromass to 1 m^2 plots, testing if it added as a net food (increasing ant colony growth and recruitment) or destroyer of habitat (by decomposing leaf litter).

2. Maximum, but not mean, colony growth rates were higher on +food plots. However, neither average colony size, nor density was higher on +food plots. In contrast, +food plots saw diminished availability of leaf litter and higher microbial decomposition of cellulose, a main component of the organic substrate that comprises litter habitat.

3. Furthermore, necromass acted as a limiting resource to the ant community only when nest sites were supplemented on +food plots in a second experiment. Many of these +food +nest plots were colonised by the weedy species *Wasmannia auropunctata*.

4. Combined, these results support the more food–less habitat hypothesis and highlight the importance of embedding studies of litter ant ecology within broader decomposer food web dynamics.

Key words. Ant colony size, decomposer food web, *Pheidole*, press experiment, scaling.

Introduction

Food limitation is the basic assumption underlying bottom-up regulation of populations (Hairston *et al*., 1960; Oksanen *et al*., 1981; Power, 1992), biomass (Sterner & Elser, 2002; Brown *et al*., 2004; Kooijman *et al*., 2004), and diversity (MacArthur, 1972; Tilman, 1982; Rosenzweig, 1996). Evidence for food limitation comes when individuals with more access to food increase rates of growth or reproduction, increase recruitment to rich patches, or both. However, studies of food limitation among terrestrial consumers rarely distinguish between growth and recruitment (but see Power, 1984; Osenberg & Mittelbach, 1996; Letourneau & Dyer, 1998).

Tropical litter ants (Hymenoptera: Formicidae) are an ideal system in which to explore the mechanisms of food limitation.

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Litter ants nest in twigs and between leaves that fall from the forest canopy (Kaspari, 1996a; McGlynn, 2006). Their small colony size (many mature with <100 workers; Wilson, 1959; Kaspari, 1996b) and frequent nest relocation (e.g. every 34–100 days; Byrne, 1994) promotes their patchiness at small scales (e.g. 0–23 colonies m^{-2}; Kaspari, 1996b). Litter ant colony growth and reproduction can be measured as the number or biomass of pupae relative to workers (Foitzik *et al*., 2004; Gammans *et al*., 2005; Fokuhl *et al*., 2007) and the presence of new reproductives (winged alates; MacKay, 1985; Deslippe & Savolainen, 1994; Aron *et al*., 2001; Bono & Herbers, 2003; Brown & Keller, 2006). If litter ants are food limited, one would predict higher growth rates, reproduction, and recruitment to supplemented plots.

However, the necromass (e.g. faeces and dead insects) that falls to the forest floor feeds the entire brown food web in which litter ants are embedded. This can lead to indirect interactions that trump direct food limitation. For

example, microbes that attack necromass may also attack the ant's leaf litter habitat. As a consequence, microbes may be both direct competitors for food and indirect competitors via the decomposition of leaf litter (Kaspari & Yanoviak, 2009). In short, any increase in decomposition—even as it feeds the brown web by converting detritus to microbial biomass—comes at the cost of decreased habitat space.

Currently, there is little evidence that food limitation accounts for the patchiness and small size of tropical litter ant colonies (Kaspari, 1996a; but see McGlynn & Owen, 2002; McGlynn, 2006). Toward a partial remedy, we report the results of a 2-month press experiment in a tropical litter food web, contrasting +food necromass plots with control plots, and those later supplemented with nest sites. We find that necromass acts most strongly as a limiting resource by enhancing recruitment when nest sites are also available.

Materials and methods

Experiments were performed from 11 May to 15 Aug 2007 on Barro Colorado Island (BCI; $9°09'$N, $79°51'$W), a lowland tropical forest managed by the Smithsonian Tropical Research Institute in Panama. BCI receives ca 2600 mm of annual rainfall, with nearly 90% falling from May to December (Croat, 1978; Leigh *et al.*, 1982). Sampling thus occurred from early to mid wet season on BCI—a period of high ant activity (Levings, 1983; Kaspari, 1996b).

Food press experiments were performed at two sites on BCI matched for habitat type, plant community and flat topography—Conrad Catchment and Barbour 9 (Leigh *et al.*, 1982). At each site, 20 control and 20 +food plots were arrayed equally along four transects, 15 m apart. The 1 m² plots were 8 m apart on each transect, and control and +food treatments were randomly assigned. Every third day, +food plots received 6 g of homogenised insects (mostly katydids, cicadas, and scarab beetles) collected at light traps, frozen, and homogenized for 1 min in a small Black and Decker food processor. Half the plots were randomly selected for harvest (equal numbers of control and +food) after 1 month and the rest were sampled after 2 months.

Litter invertebrates (e.g. Acari, Araneae, Collembola, Coleoptera, Diplopoda) were extracted with Berlese funnels from the leaf litter of 10 control plots harvested on 12 August 2007. The standing crop dry biomass of these organisms ranged from 0.09 g to 1.2 g m⁻². Thus, 6 g insect necromass addition per m² represented a substantial increase over ambient conditions.

Prior to food addition, baiting trials were performed to confirm that ants harvested insect necromass. At both sites, 20 baiting stations were placed adjacent to experimental plots at 5 m intervals along two parallel transects. Each baiting station consisted of 4 g insect necromass, placed on a 3×5 in. note card and checked for ants after 45 min and 1.5 h.

Ant colonies were harvested after 1 and 2 months by searching all leaf litter in plots and cracking all twigs and seedpods, using a headlamp when necessary (approximately one plot harvested h⁻¹; as per Kaspari, 1996a,b). Colonies

were stored in plastic bags. Back at the laboratory, colonies were identified and surveyed for larvae, pupae, workers, queens, male and female alates using a dissecting scope. After counting, all components were frozen, dried at $60\,°C$ for 2 days and then weighed to the nearest 1 µg. Vouchers of species and morphospecies (henceforth species) are deposited in the collection of the second author at the University of Oklahoma.

Do ants grow and reproduce more on +food plots?

To test for higher growth rates on +food plots, pupae–worker curves were constructed (as per Kaspari, 1996b) for species with ≥15 colonies on both food and control plots and for all colonies with queens. These curves characterised the dependence of pupae number (y) on worker number (M) using ordinary least square regression to estimate a and b in the scaling equation $\log_{10} y = \log_{10} a + b \log_{10} M$. To test the null hypothesis of isometry (H$_0$: $b = 1$), F-statistics were calculated. ANCOVAS were used to examine variation in scaling exponents (b) across feeding treatments. The relationships between worker number and pupae number sometimes yielded triangular relationships suggesting constraint functions (Brown, 1995; Cade & Noon, 2003). To test whether food addition removed an upper constraint on colony growth, least absolute deviation regression was used to describe scaling for the upper 90th quantiles of these plots (Cade & Richards, 2005; Koenker, 2005).

Using $\log_{10}$ transformed data, we also tested for increasing colony size (worker number or dry biomass of workers, pupae, and queens) with food addition among the common species and across all colonies with queens. ANOVA was used to test whether colony size increased on +food plots from month 1 to 2, and ANCOVA was used to test whether food addition increased mean colony size m⁻² after controlling for litter depth. Finally, as reproductives were relatively rare, the biomass of reproductives on control and +food plots was compared using a non-parametric Mann–Whitney test.

Do ant colonies accumulate on +food plots?

Using $\log_{10}$ transformed data, ANOVA was performed to test whether food addition increased the density of nests m⁻² after 1 and 2 months. ANCOVA was then performed with litter depth as a covariate.

Does litter habitat decompose more quickly on +food plots?

Litter depth (two corners and plot centre) was recorded at the outset and harvest of each plot using a ruled PVC rod inserted through litter to mineral soil. In each plot, decomposition rates were estimated during the first month by measuring mass lost from two discs (96 mg) of coarse filter paper (100% cellulose, Fisher 09-795C) inserted in 10×10 cm polyester litterbags and placed under leaf litter (as per Milton & Kaspari, 2007). These closed litterbags excluded taxa larger than 100 µm and thus provided estimates of microbial decomposition. After

1 month in the field, the remaining cellulose was harvested, dried for 2 days at 60 °C, and mass loss measured to the nearest 0.01 g. We tested if mass loss of cellulose increased (ANOVA), and litter depth decreased (paired *t*-test on *initial – final* litter depth) on +food plots.

Next, artificial nest sites were added to test whether providing important components of habitat structure would enhance recruitment to +food plots. Once plots were harvested after both 1 and 2 months, we (1) returned litter (without colonies and their nest sites) to these plots and (2) added four artificial nests (8 cm × 0.25 cm hollow bamboo internodes) to 0.25 m² zones within the original plots. Previous experiments have shown that litter ants readily colonise hollow internodes (e.g. Herbers, 1986; Kaspari, 1996b; Armbrecht *et al.*, 2004). These bamboo-seeded plots were maintained as +food (4 g homogenised insects added every 3 days) or control. Half of these plots were harvested after 2 weeks and the rest after 1 month. Colonies were collected from bamboo and processed as above.

Results

Overall, 634 colonies (298 control, 335 +food) were harvested from 80 1-m² plots. Of the 63 species collected from 24 genera (see Table S1), 20 occurred only once (11 on +food, 9 on control plots). Species richness did not differ between control (mean: 4.6 ± 2.0; range: 1–9 species) and +food plots (mean ± SD: 5.6 ± 2.9; range: 1–15 species) (ANOVA: $F_{1,77} = 2.61$; $p = 0.11$). Seven species (*Cyphomyrmex rimosus* Spinola 1851, *Solenopsis* sp. 2, *Solenopsis* sp. 3, *Pheidole multispina* Wilson

2003, *Pheidole rugiceps* Wilson 2003, *Pheidole ruida* Wilson 2003, and *Pyramica brevicornis* Mann 1922) were found ≥15 times on both +food and control plots and met our criteria as 'common'.

Ants rapidly mobilised at necromass baits and 95% were occupied after 45 min. All common species except *P. brevicornis* and *C. rimosus* were observed at baits. Overall, baiting once per site (for only 1.5 h) yielded 24 species (60% of all harvested colonies) and 12 genera (76% of all harvested colonies).

Of all sampled colonies, 394 had queens (control plots: 189; +food plots: 205) and 43 of these were lone foundress queens (control plots: 18; +food plots: 25). The queen colony subset was used to measure population-level responses to food addition, and all harvested colonies were used for community-level analyses of biomass. As ant community structure and colony responses to food addition were consistent across the two sites on BCI, data were combined for analyses.

Do ants grow and reproduce more on +food plots?

Least square regression analyses of all harvested colonies with queens suggested that growth did not increase with food addition. First, pupa–worker curves did not differ between colonies from control ($b = 0.70$) or +food ($b = 0.79$) plots (Table 1). Second, the slope for the growth curve remained significantly less than isometry after food addition (*F*-test for $b = 1$: $F_{1,203} = 21.22$, $p = 0.0001$) (Table 1). However, the triangular nature of these relationships (Fig. 1) suggested that worker number was necessary, but not sufficient to explain

Table 1. Ordinary least squares (OLS) and least absolute deviation (LAD) regression for scaling of pupae number against worker number ($y = aM^b$).

| Species | TRT | n | Linear regression | | | | | | | | Quantile regression (upper 90th quantile) | | |
			F	R²	a	SE	b	SE	± 95% CI of b	b	SE	p
C. rimosus	C	25	5.90	0.20	−0.30	0.29	0.54*	0.22	0.46	0.51	0.41	0.04
	F	22	5.35	0.21	−0.13	0.26	0.49*	0.21	0.44	NS	NS	NS
Solenopsis sp. 2	C	19	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	F	29	7.10	0.21	−0.18	0.45	0.86	0.32	0.66	0.84	0.34	0.02
Solenopsis sp. 3	C	28	40.75	0.61	−0.77	0.36	1.28	0.20	0.41	0.73	0.42	0.002
	F	29	50.25	0.65	−1.45	0.41	1.62*	0.23	0.47	1.16	0.40	0.02
P. multispina	C	24	8.57	0.28	−0.22	0.38	0.72	0.25	0.51	0.75	0.20	0.02
	F	21	26.58	0.58	−0.29	0.26	0.91	0.18	0.37	0.88	0.32	0.04
P. rugiceps	C	17	25.57	0.63	−0.07	0.26	0.80	0.16	0.34	0.88	0.17	0.05
	F	25	14.83	0.40	−0.16	0.31	0.75	0.19	0.40	0.85	0.27	0.04
P. ruida	C	32	32.20	0.52	−0.14	0.24	0.78	0.14	0.28	0.66	0.20	0.02
	F	28	34.58	0.57	−0.30	0.25	0.89	0.15	0.31	0.99	0.14	0.02
P. brevicornis	C	15	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
	F	16	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Queen colonies	C	189	162.11	0.46	−0.09	0.08	0.70****	0.05	0.11	0.71	0.08	0.0001
	F	205	318.31	0.61	−0.15	0.06	0.79****	0.04	0.08	0.91	0.05	0.0001

For OLS regressions, significant deviation of slope from isometry ($b = 1.0$) denoted by *($P = 0.05$), **($P = 0.01$), ***($P = 0.001$), ****($P = 0.0001$). For LAD regressions, *p* values indicate whether slope *b* differs significantly from zero. *n* denotes number of samples in analysis. Treatment (TRT) groups are colonies harvested from control (C) or +food (F) plots. Queen colonies include all harvested colonies with queens. NS indicates non-significance of overall model.

Table 2. Results from ANCOVAs testing effects of treatment (food addition vs control) on the scaling of $\log_{10}$(pupae number) on $\log_{10}$(worker number). In no case did average colony growth rate (i.e. pupae worker ratio) increase on food plots.

Species	Factor	d.f.	Type III SS	*F*	*p* > *F*
C. rimosus	Treatment (TRT)	1	0.025	0.20	0.66
	Worker number	1	1.429	11.16	0.002
	TRT × Worker number	1	0.004	0.03	0.87
	Error	43			
Solenopsis sp. 2	Treatment	1	0.785	2.63	0.11
	Worker number	1	0.529	1.77	0.19
	TRT × Worker number	1	0.814	2.73	0.11
	Error	44			
Solenopsis sp. 3	Treatment	1	0.342	1.55	0.22
	Worker number	1	20.160	91.25	0.0001
	TRT × Worker number	1	0.271	1.23	0.27
	Error	53			
P. multispina	Treatment	1	0.006	0.02	0.88
	Worker number	1	7.324	28.66	0.0001
	TRT × Worker number	1	0.098	0.38	0.54
	Error	41			
P. rugiceps	Treatment	1	0.009	0.04	0.84
	Worker number	1	7.380	33.89	0.0001
	TRT × Worker number	1	0.009	0.04	0.84
	Error	38			
P. ruida	Treatment	1	0.037	0.21	0.65
	Worker number	1	11.755	67.13	0.0001
	TRT × Worker number	1	0.045	0.26	0.61
	Error	56			
P. brevicornis	Treatment	1	0.102	0.66	0.42
	Worker number	1	0.857	5.16	0.03
	TRT × Worker number	1	0.082	0.49	0.49
	Error	26			
Colonies with queens	Treatment	1	0.093	0.43	0.51
	Worker number	1	97.415	452.97	0.0001
	TRT × Worker number	1	0.396	1.84	0.18
	Error	393			

Fig. 1. Scaling of $\log_{10}$(pupae number) against $\log_{10}$(worker number) across all colonies with queens, with slopes (*b*) from ordinary least squares (OLS) regressions. Each data point represents a single colony. Open circles and dashed lines, control (C); closed circles and solid lines, +food colonies (F). Grey lines are least absolute deviation (LAD) regressions through the 90th quantile drawn as per treatment.

+food plots, but these were not significantly different from their respective control plot curves (Table 2). Regressions through 90th quantiles yielded slopes that were generally within <0.10 of slopes from least square regressions (Table 1). Notable exceptions were colonies of *S*.sp. 3 and *P. ruida* from +food plots (Fig. 2) that, respectively, had 90th quantile slopes 0.43 and 0.33 greater than control plot colonies (Table 1). For these species, food addition may have relieved an upper constraint on colony growth.

The number of workers per colony and mean colony biomass increased on all plots by month 2, but colonies on +food plots were not larger than those from control plots (Table 3). Likewise, total colony biomass summed per m² increased 31% across all plots by month 2 (from 21.7 ± 18.9 to 31.5 ± 23.2 mg m⁻²; ANOVA: $F_{1,77}$ = 5.12, *p* = 0.03). However, none of the focal species had significantly larger colonies after 2 months.

Overall, 54 colonies had reproductive adults or pupae (24 control, 30 +food). Colonies on +food plots (lower quartile, median, upper quartile: 0.00, 0.00, 0.85 mg) did not yield more reproductive biomass than those from control plots (0.00, 0.06, 0.97 mg) (Mann–Whitney *U* = 1604; *n* = 40,41; *p* = 0.72). In addition, control (18 of 40) and +food (22 of 40) plots were equally likely to house reproducing colonies ($\chi^2_{0.05,1}$ = 0.8, *p* = 0.37).

Do ant colonies accumulate on +food plots?

Nest density did not increase with food addition (Table 3) and averaged 7.5 ± 4.4 nests m⁻² (range: 1–20) on control plots and 8.2 ± 4.6 (range: 2–22) on +food plots. Litter depth was not a significant covariate explaining nest density (Table 3). Among common species, only nest densities of *P. ruida* increased with litter depth (ANCOVA: $F_{1,75}$ = 10.12, *p* = 0.002).

variation in pupae number across colonies. At the 90th quantile, the upper edge of this triangle, the slope (b ± 95% CI) from +food plot colonies (0.91 ± 0.13) overlapped with isometry and was 0.2 greater than the slope for control colonies (0.71 ± 0.2) (Table 1).

Growth curves following food addition varied considerably among common species (Fig. 2), including slopes significantly less than (b = 0.49; *C. rimosus*) and significantly greater than (b = 1.62; *S*. sp. 3) isometry (Table 1). Colonies of *P. multispina* and *P. ruida* had steeper growth curves on
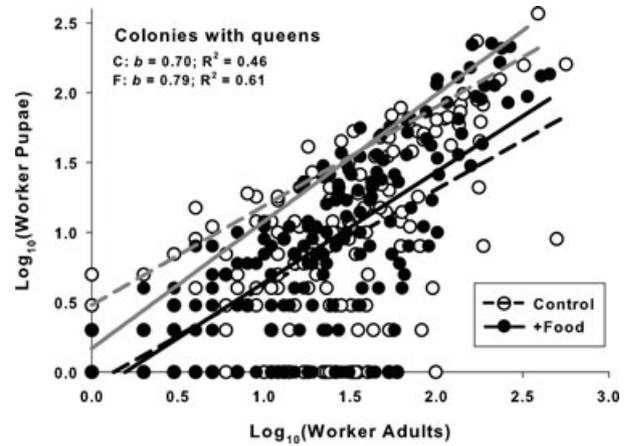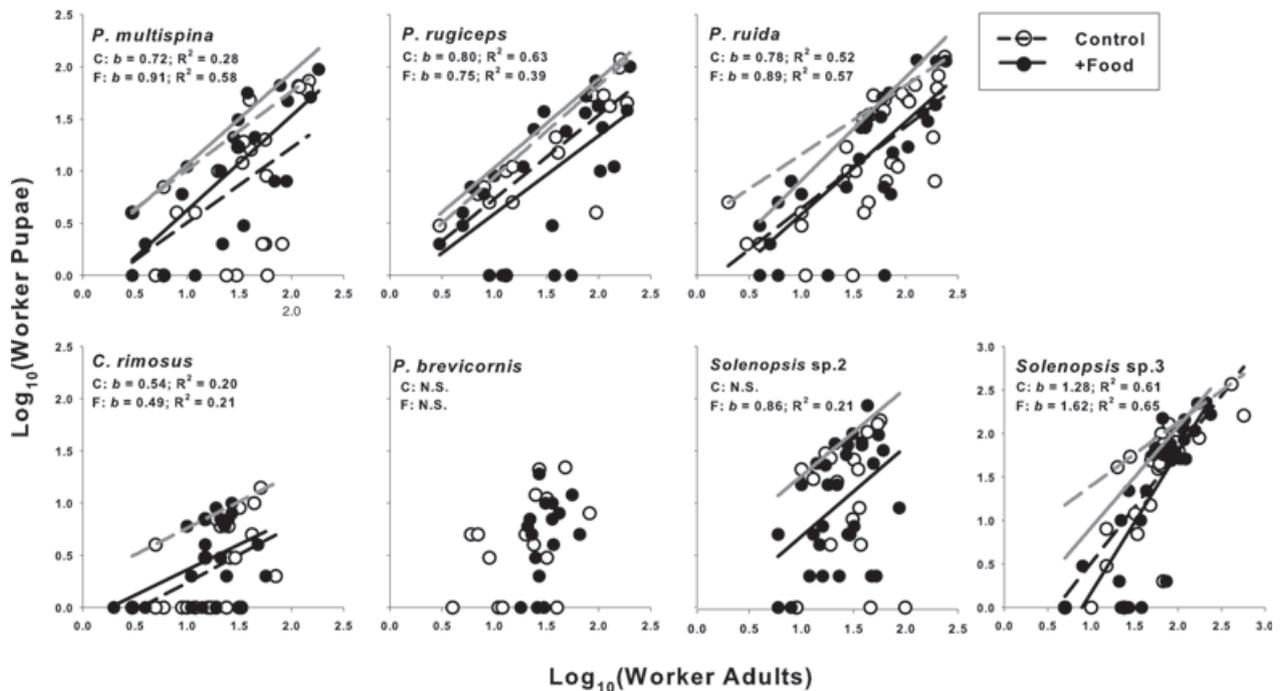
Fig. 2. Scaling of pupa number against worker number for common species. See Fig. 1 caption for details.

Table 3. Analyses of food limitation of colony growth (mean worker number m^{-2} or mean colony biomass m^{-2}) and recruitment (nest density m^{-2}) using $\log_{10}$ transformed data. Colony biomass measured per colony as sum of worker, pupae, queen dry mass (mg).

Effect	Test	Factor	d.f.	Type III SS	F	p > F
Mean worker number	ANOVA	Month	1	0.408	5.28	0.02
		Treatment	1	0.051	0.67	0.42
		Month × Treatment	1	0.070	0.90	0.35
		Error	77			
	ANCOVA	$\log_{10}$(litter depth)	1	0.085	1.09	0.30
		Treatment	1	0.050	0.63	0.43
		$\log_{10}$(litter depth) × Treatment	1	0.073	0.93	0.34
		Error	75			
Mean colony biomass	ANOVA	Month	1	0.096	4.94	0.03
		Treatment	1	0.000	0.01	0.92
		Month × Treatment	1	0.046	2.36	0.13
		Error	77			
	ANCOVA	$\log_{10}$(litter depth)	1	0.011	0.54	0.46
		Treatment	1	0.067	0.32	0.58
		$\log_{10}$(litter depth) × Treatment	1	0.006	0.31	0.58
		Error	75			
Nest density	ANOVA	Month	1	0.070	1.36	0.25
		Treatment	1	0.040	0.77	0.38
		Month × Treatment	1	0.001	0.00	0.99
		Error	77			
	ANCOVA	$\log_{10}$(litter depth)	1	0.124	2.47	0.12
		Treatment	1	0.066	1.31	0.26
		$\log_{10}$(litter depth) × Treatment	1	0.102	2.03	0.16
		Error	75			

Does litter habitat decompose more quickly on +food plots?

Three pieces of evidence suggest that habitat space declined on +food plots. First, microbial decomposition of cellulose averaged 15% higher on +food plots (mean mass loss +food: 687 mg vs control: 599 mg; $F_{1,76} = 4.17$, $p = 0.045$). Second, food addition accelerated a seasonal decline in habitat availability: litter depth decreased 30% on +food

plots (from 2.5 to 1.7 cm, $t_{39, 0.05} = 5.22$, $p = 0.0001$), but decreased only 12% on control plots (from 2.3 to 2.1 cm, $t_{37, 0.05} = 1.62$, $p = 0.11$). Finally, although nest densities did not previously increase on +food plots (see above), artificial nests were colonised twice as frequently when combined with food addition than when added alone ($\chi^2_{0.05, 1} = 12.5$, $p = 0.0001$; Fig. 3). Nearly half of all colonisation on +food plots was by queenless satellite nests of *Wasmannia auropunctata* (Roger 1863).

Discussion

Contrary to the food limitation hypothesis, colony size, number, and total biomass were not enhanced on +food plots relative to controls. Instead, food addition may have indirectly impacted this tropical litter ant community in ways that support the 'more food, less habitat' hypothesis. First, food addition simultaneously increased rates of microbial decomposition and decreased litter availability. Second, we only detected food limitation when we added nest sites and thus reduced the ability of decomposer taxa to destroy habitat. In summary, the picture of how resources limit tropical litter ant colonies should increasingly come into focus as studies integrate decomposer food web dynamics, tracking how food flows from microbes to ants.

The present results contrast with other studies reporting enhanced colony growth (e.g. Fokuhl *et al.*, 2007) and reproduction (e.g. Deslippe & Savolainen, 1994; Aron *et al.*, 2001; Brown & Keller, 2006) following experimental food addition. However, many of the previously studied ecosystems are in temperate regions, including English heath lands (Gammans *et al.*, 2005), southern Californian chaparral (MacKay, 1985), and temperate woodlands (Bono & Herbers, 2003). Species in these studies excavate nests as subterranean galleries that are unlikely to be degraded by decomposer taxa, such that

food addition may be less closely tied to the availability of habitat space.

McGlynn (2006) performed the only other food addition experiment in a tropical litter ant community, adding 5 g of termites covered in vegetable oil m^{-2} at 2-day intervals. After 4 months, a total of ca 300 g necromass m^{-2} increased nest densities relative to controls. In this study, adding both food and nests more than doubled colonisation relative to control after only 1 month and ca 40 g necromass 0.5 m^{-2}. Thus, although food limitation appears to limit litter ant colony density within tropical forests, the availability of leaf litter habitat may constrain colony access to food patches.

In tropical forests, food limitation appears necessary, but not sufficient to explain patterns of colony size. Although least square regressions did not detect treatment differences between colony growth curves (Table 2), the triangular shape of many of these relationships suggested an upper constraint on relative investment in worker pupae, with unmeasured variables generating scatter below this line (Brown, 1995; Cade & Noon, 2003). At the 90th quantile, colonies yielded increasingly more pupae on +food plots ($b = 0.91 \pm 0.13$) relative to those from control plots (0.71 ± 0.20) (Fig. 1).

In this study, at least three additional factors independent of colony size may have reduced growth below the 90th quantile. The first is natural interspecific variation in growth rate (Fig. 2), some of which may be due to dietary variation among species in diverse tropical litter ant communities (Tobin, 1994; Wilson, 2005). Second, raids by predators like army ants occur daily at the m^2 scale in the most productive tropical forests (Kaspari & O'Donnell, 2003), and may empty nests of their brood. Third, soil-nesting species with aggressive workers (e.g. *Odontomachus bauri* Emery 1892 and *Ectatomma ruidum* Roger 1860) may also have harvested some fraction of added food. At both sites, foraging workers of *E. ruidum* recruited to 58% of necromass baits after 1.5 h. Experimental removal
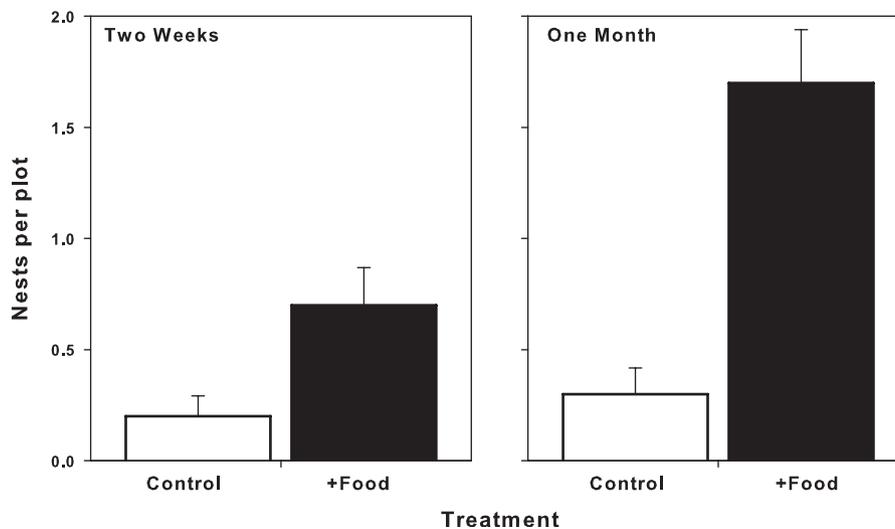

Fig. 3. Colonisation of artificial ant nests on +food and control 0.25 m^2 plots after 2 weeks and 1 month. Each bar represents the mean (+1 SE) of 20 plots.

of these colonies should go far in quantifying their influence (Gibb & Hochuli, 2004).

Although diversity did not change with food addition, habitat loss on these plots may have confounded recruitment dynamics. Interestingly, satellite nests of *W. auropunctata* increasingly recruited to +food plots when we mitigated habitat loss by also adding nests. Although BCI is likely within the native range of *W. auropunctata* (Tennant, 1994; Wetterer & Porter, 2003), it is a highly invasive weedy species that displaces native taxa when introduced into novel tropical habitats (Clark *et al.*, 1982; Le Breton *et al.*, 2003). Although foraging workers in native populations of *W. auropunctata* do not appear numerically or behaviourally dominant at resource baits (Tennant, 1994; Orivel *et al.*, 2009), whole colonies may be predisposed for invasive success because their decentralised nests quickly colonise ephemeral resource patches. Furthermore, the environmental heterogeneity hypothesis predicts decreasing diversity when resource addition diminishes niches of low resource use (Rosenzweig *et al.*, 1984; Tilman & Pacala, 1993). Further studies should shed light on whether *W. auropunctata*, a species with low nitrogen use efficiency (Davidson, 2005), excludes other taxa in native forests by dominating available nitrogen (e.g. Wedin & Tilman, 1993).

Conclusions

The quality of +food plots in this study may have been diminished by enhanced decomposer activity that degraded the structure of leaf litter habitat (e.g. Jonasson *et al.*, 1996). Experimental nutrient addition has previously enhanced decomposition rates across tropical forests with weathered soils (Hobbie & Vitousek, 2000; Kaspari *et al.*, 2008). When we added nutrients packaged as insect necromass, decomposer activity increased and colonies recruited to +food plots only when we also added nests (Fig. 3). Thus, tropical litter ants may simultaneously be limited by the availability of food (McGlynn, 2006) and patchy leaf litter that becomes increasingly ephemeral when saturated with food (Kaspari & Yanoviak, 2009). Needed now is a more detailed picture of the specific aspects of litter habitat (e.g. nest sites) most impacted by decomposer microbes, and the biological pathways through which this occurs.

Acknowledgements

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: DOI 10.1111/j.1365-2311.2009.01165.x

Table S1. List of species collected during this study.

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