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Using nutritional ecology to predict community structure: a field test in Neotropical ants

Michael Kaspari,[1,2,]† David Donoso,[1,4] Jane A. Lucas,[3] Taylor Zumbusch,[3] and Adam D. Kay[3]

[1]*Graduate Program in EEB, Department of Biology, University of Oklahoma, Norman, Oklahoma 73019 USA*
[2]*Smithsonian Tropical Research Institute, Balboa, Republic of Panama*
[3]*Department of Biology, University of St. Thomas, St. Paul, Minnesota 55105 USA*
[4]*Museo de Zoología QCAZ, Escuela de Ciencias Biológicas, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre 1076 y Roca, Apdo 17-01-2184, Quito, Ecuador*

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Abstract. Nutritional ecology predicts consumer behavior based on the biochemistry of species and biogeochemistry of the environment. It is thus well suited as a tool for predicting the effects of specific nutrients on consumer activity, abundance, and diversity across the landscape. We tested hypotheses from nutritional ecology in a Neotropical litter ant community by supplementing forest plots with carbohydrates (CHOs) and protein in a blocked factorial design. We tested the *Compensation Hypothesis*, which posits that consumers accumulate in patches of the rarest food type relative to demand, and the *Economics Hypothesis*, which assumes that species differ in nutrient based-functional traits, and that changes in nutrient availability will generate changes in species composition and community behavior. We found that CHO and protein had distinct effects on ant density, community composition, and per-worker activity. Ant density increased by 35% on +CHO plots but not +Protein plots, a result supporting the Compensation Hypothesis because CHO-rich plant exudates are uncommon and CHO-demanding microbial productivity is high in this brown food web. Consistent with the Economics Hypothesis, we found that +CHO plots had higher per-capita ant activity (the *Metabolic Fuel Hypothesis*) and attracted ants averaging 10% lower δ^{15}N values. Species composition changed as well, with *Wasmannia auropunctata*, an invasive outside its native range, elsewhere, increasing five-fold on +CHO plots. Nutritional ecology can thus account for some of the patchiness and behavior of consumers in diverse communities.

Key words: ants; brown food web; carbohydrates; Economics Hypothesis; functional traits; Liebig's Law of the Minimum; litter; Metabolic Fuel Hypothesis; nitrogen; nutritional ecology; protein; stoichiometry.

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† **E-mail:** mkaspari@ou.edu

INTRODUCTION

Community ecology's "bottom up" school matches the availability of resources with the per-capita use of resources to predict how species array along resource gradients (MacArthur 1972). Its early work focused on how bulk foods or single currencies (e.g., energy) affected community patterns (Pulliam 1985, Brown 1989, Sevenster and Van Alphen 1993, Chesson and Huntley 1997, Ritchie and Olff 1999). More recently, ecological stoichiometry (Sterner and Elser 2002, Kaspari 2012) and nutritional ecology (Simpson and Raubenheimer 2001, Simpson et al. 2004) have explored how the availability of a mix of biochemicals, and their contribution to the niche, combine to generate patterns of diversity and abundance. By abstracting ecosystems into packages of elements and compounds, one goal of nutritional ecology is to generate a theory of community ecology from biochemical first principles.

Carbohydrates and proteins (henceforth "CHO" and "Protein") are two classes of compounds with distinctive chemistries (C, H, and O, vs. C, H, O, P, N, and S) and complementary functions. CHO and Protein have been frequent currencies in bottom-up theory based on Leibig's Law of the Minimum (Liebig 1855). For example, small endotherms with relatively high energy requirements are predicted to select prey that maximize the intake of CHOs (Stephens and Krebs 1986); they consequently accumulate in high CHO patches (Pimm et al. 1985). Likewise herbivore taxa are predicted to be protein-stressed (White 1993); herbivores also often accumulate in high protein patches (Heidorn and Joern 1984, Elser et al. 2000).

Nutritional ecology moves beyond Leibig to emphasize the interactive effects of dietary CHO and Protein on animal performance and how these effects can differ among consumer taxa (Behmer 2008, Raubenheimer et al. 2009, Simpson et al. 2010). Here we explore its potential to turn maps of CHO and Protein availability into patterns of diversity and abundance in consumers.

Tropical ant communities as subjects of bottom-up experiments

Tropical litter ant communities are a tractable testing ground for nutritional ecology. Such communities can respond rapidly to experimental treatments as litter ants exist at high densities (ca. 5 colonies/m^2, Kaspari 1996) of mostly small colonies (ca. 10–1000 workers, Kaspari 2005) that can relocate once every two weeks (Byrne 1994). There is evidence for strong responses of ant abundances to food supplements in this system, as shown by studies using bulk insect addition (McGlynn 2006, Shik and Kaspari 2010). In addition, a large fraction of ant species are facultatively omnivorous (Kaspari et al. 2000), collecting both CHO- and Protein-rich resources (Bestelmeyer et al. 2000). CHO and Protein serve different needs within an ant colony (Weeks et al. 2004, Bluthgen and Feldhaar 2010) and interspecific differences in trophic level and C:N chemistry can potentially translate into interspecific differences in nutritional needs (Yanoviak and Kaspari 2000, Blüthgen et al. 2003, Davidson 2005). Here we field-test hypotheses derived from stoichiometry toward predicting patterns in ant abundance, diversity, and activity in the tropical litter.

Hypotheses

The *Compensation Hypothesis* (Kaspari and Yanoviak 2001, Davidson 2005) uses the logic of Liebig's Law of the Minimum (Liebig 1855). It assumes the utility of a resource is invariant across species and varies only with availability; it predicts a single limiting resource that is locally in shortest supply. Hence as CHO availability increases, the marginal value of CHO decreases relative to other potentially limiting resources like Protein. As a consequence, habitats with relatively high Protein availability should support ants that are more attracted to CHOs; and vice versa. This proved true in a comparison of ant behavior in the CHO-rich tropical canopy versus the relatively protein rich litter below. In a choice experiment, canopy ants preferred Protein baits over CHO baits 9:1 compared to 1:1 use in the litter (Kaspari and Yanoviak 2001).

The *Economics Hypothesis* (Yoshida 2006) uses the logic of Levins' (1968) fitness sets, and predicts that as the availability of a resource increases, investments to traits rich in that resource should also increase. Thus, populations of herbivores, with diets rich in CHO should have (1) high whole body [C], and (2) heavy investment in C-based traits. Predators, in turn, with N-rich diets, should have higher whole body [N] (Fagan et al. 2002, Davidson 2005) and in turn rely on N-rich functional traits. A specific case is the *Metabolic Fuel Hypothesis* (Davidson 1997, Kay et al. 2010), which predicts that surpluses of CHOs are invested in higher activity rates (or "tempo" sensu Oster and Wilson 1978). For example, high CHO habitats like the tropical canopy support relatively quick and aggressive ant assemblages compared to the more Protein-rich tropical litter (Davidson 1997, Yanoviak and Kaspari 2000, Davidson et al. 2003, Gibb and Cunningham 2009). In the lab, colonies fed high-CHO diets increased tempo and/or aggression (Grover et al. 2007, Kay et al. 2010) although in Kay et al., higher colony tempo resulted from more, not faster workers. These logical connections between diet, traits, and fitness yield the prediction that herbivores and C-based traits (e.g., tempo) should increase on +CHO plots.

Nutritional ecology potentially has much to say about the structure and function of ecological communities. Yet we know of no field experiments exploring how the abundance, diversity, and activity of a species assemblage varies with CHO:Protein ratios. Here we use a field experiment in a Panama litter ant community to evaluate the predictions of the Compensation, Economics, and Metabolic Fuel Hypotheses. To accomplish this, we use a factorial design that offers litter ants CHO, Protein and CHO + Protein in an agar base over 30–60 days.

METHODS

We conducted this work in May-July 2009 on Barro Colorado Island, (BCI; 9°09′ N, 79°50′ W), a lowland, seasonally wet forest in Lake Gatun of the Panama Canal. BCI has a long history of ant studies (Levings and Franks 1982, Kaspari 1996, Feener and Schupp 1998) and a well-documented fauna of ca. 400 species (Donoso in prep). We conducted the study along the Thomas Barbor trail at markers 8–9. The experiment coincided with the beginning of the wet season, a period of increased ant activity and a flush of litter resources (Levings and Windsor 1996).

Nutrient supplementation

We used a factorial design to test main and interactive effects of CHO and Protein on litter ant communities. The experiment consisted of 30: 2×2 m blocks, with a 0.25 m^2 plot in each corner. Plots within blocks were randomly assigned one of four supplementation treatments: +H2O, +CHO, +Protein, +CHO + Protein. We used synthetic foods from previous ant nutrition studies (Dussutour and Simpson 2009, Kay et al. 2012). Supplements were agars (80 mg/ml): 10% (w/v) sucrose food (CHO); a 10% protein food (Protein), which consisted of equal parts whey protein isolate, calcium caseinate, and whole egg powder; a mixed food with 10% sucrose and 10% protein (CHO + Protein); and water. The use of synthetic foods allowed us to precisely manipulate food quality; it also allowed us to create a uniform food base for testing the interactive effects of CHO and Protein consumption on community traits. On each 0.25 m^2 plot, we placed 1.2 g pieces of agar on 4 separate 2-cm^2 notecards (placed 15 cm apart around the center of the plot). We provided these foods for 2 hr every second day for 30 days (for 20 blocks) or 60 days (for 10 blocks). We assayed feeding behavior every 4 days by counting the number of ants feeding on each food piece after 1 hr. Because the ant community at this site is diverse and workers of many species are too small to identify in the field, we coarsely classified feeding ants by size (small <3 mm length or large >3 mm).

Assessing activity rate

After 30 days, we determined how food addition affected community-level activity. To assay activity, we placed five 10-cm long wooden tongue depressors in a grid in the center of each plot. We counted the number of small ants and larger ants that appeared on the top (visible portion) of the grid over the course of 1 min.

Monitoring ant abundance and composition of plots

To explore how ant abundance and composition responded to food addition, we harvested plots from 20 randomly selected blocks after 30 days, and the remaining 10 blocks after 60 days. All extractions took place 2 days after the last baiting. Litter was collected down to mineral soil and run through a berlese funnel to extract ants. Ants were identified to species or morphospecies and worker density was quantified as ants/0.25 m^2.

Whole body nitrogen and trophic analyses of ants

We quantified percentage of whole body N content and stable isotope ratios of common ants to explore how response to food addition was associated with ant composition or trophic position, respectively. All samples were workers not subject to experimental feeding (e.g., from +H_2O plots, or other collections on BCI) that had been collected in 95% EtOH within the previous year and their gasters removed. Samples were dried at 60°C and sealed in tin capsules. We measured N content using a Flash EA1112 CN analyzer (ThermoQuest, Milan, Italy) that completely combusts samples; we used aspartic acid as a standard. Stable isotopes were analyzed at the University of Oklahoma or University of Utah using a CosTech Elemental Analyzer interfaced through a ConFlo III open split valve with a Thermo Finnigan Delta V isotope ratio mass spectrometer. N isotope values are reported using delta notation ($\delta^{15}N$) where $\delta = ((R_{\text{sample}}/R_{\text{standard}}) - 1) \times 1000$; R = ratio of heavy to light isotope ($^{15}N/^{14}N$) of the sample and standard. Delta values are expressed in ‰ (per mil notation). We used a laboratory standard referenced against the international standards for N of atmospheric nitrogen giving us a stable isotope precision of ± 0.32‰ ($N = 4$).

Statistics

Our analysis exploited the block design (treating one and two month samples equally) using both parametric (SAS 2006) and nonparametric (McCune and Mefford 2011) tests where appropriate. We first tested the effects of our bait treatment on bait use over the course of the experiment using repeated-measures ANOVA. We then contrasted ant density among food additions with a factorial ANOVA (CHO and Protein) and a blocking factor.

The Compensation Hypothesis assumes all species in a community respond to nutrients similarly; while the Economics Hypothesis assumes resource specialization governed by tradeoffs. To examine the role of the food additions on species diversity and composition, we used the same analysis as for density, but added a nonparametric PERMANOVA (Anderson 2001), using Bray Curtis distance, to contrast the role of block and treatment on the composition of the six species found on 50% or more of the plots. PERMANOVAs are multivariate analyses of variance that use permutations to generate P-values (Anderson 2001).

We tested the Compensation Hypothesis prediction of higher ant densities on +CHO plots using a factorial ANOVA. We tested the Metabolic Fuel Hypothesis by contrasting the number of ants appearing on the wooden platform in 1 minute on plots after 30 days. Since worker density (harvested at 30 or 60 days) was shown to increase on +CHO plots, we used it as a covariate to generate a measure of per-ant activity.

We contrasted the Economics and Compensation Hypothesis—using the factorial ANOVA with blocks—by examining how the average ant harvested from a plot varied in trophic level ($\delta^{15}N$) and percent whole body N. To do this, we characterized each plot by the average species values of $\delta^{15}N$ and %N for those species harvested from that plot, weighted by their density.

RESULTS

A total of 77 species, including 6 subfamilies and 32 genera, was recorded from the 120 plots (Appendix A). Fifteen species from 7 genera, mainly of the subfamily Myrmicinae, made up 90.2% of workers sampled: *Solenopsis* (6 species), *Pheidole* (3), *Cyphomyrmex* (2), *Wasmannia* (1), *Nylanderia* (1), *Pyramica* (1), and *Octostruma* (1).

Use of ant baits over the course of the experiment

Consistent with the Compensation Hypothesis, more ants visited baits in +CHO plots than +Protein plots (Fig. 1). Both small and large ants visited CHO baits more than water controls (small: $F_{1,87} = 12.5$, $p < 0.0001$; large: $F_{1,87} = 31.3$, $p < 0.0001$), but this was not true for Protein baits (small: $F_{1,87} = 1.9$, $p = 0.173$; large: $F_{1,87} = 2.3$, $p = 0.130$), nor was there a significant CHO-Protein interaction (small: $F_{1,87} = 2.3$, $p = 0.137$; large: $F_{1,87} = 0.3$, $p = 0.590$). Moreover visits to Protein baits generally decreased over the course of the experiment (time-Protein interaction: small: $F_{5,83} = 2.4$, $p = 0.047$; large: $F_{5,83} = 2.4$, $p = 0.008$), but activity at CHO baits was invariant over the same period (time-CHO interaction small: $F_{5,83} = 1.5$, $p = 0.210$; large: $F_{5,83} = 0.6$, $p = 0.716$). These patterns of bait use were consistent across the study site (block effects- small: $F_{29,87} = 0.9$, $p = 0.585$; large: $F_{29,87} = 1.0$, $p = 0.448$).

Density and diversity at the close of the experiment

Consistent with the Compensation Hypothesis, ant density in the litter increased on +CHO plots but not +Protein plots (Fig. 2, Table 1). Berlese extraction yielded 15,514 ants, from 77 species. Worker density in the 0.25 m^2 plots varied over 100 fold (1–750 workers/0.25 m^2) and varied across the 30 blocks from a least squares mean of 43 to 289 ants/0.25 m^2 ($p = 0.0003$, Fig.

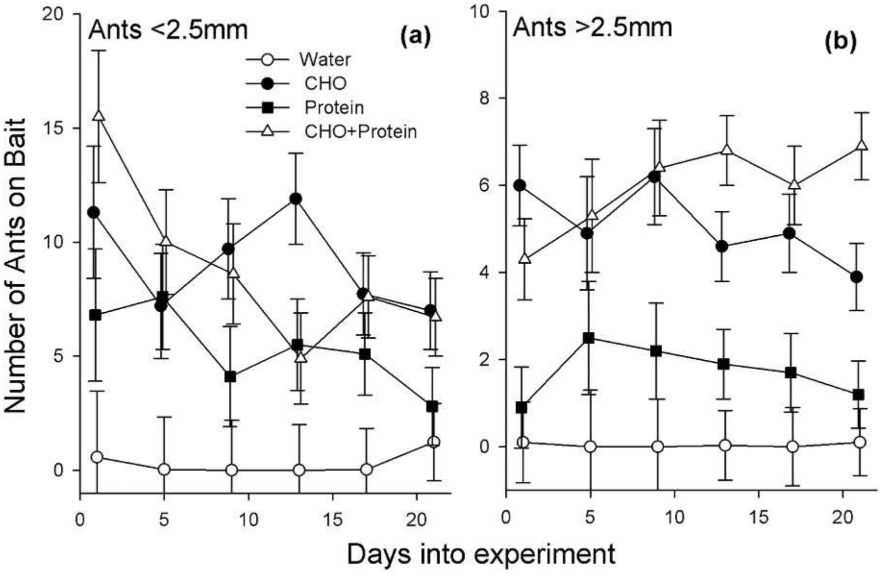

Fig. 1. Bait use by small (a) and large (b) tropical litter ants (least square means ± 1 SE) on plots supplemented with water, carbohydrates (CHOs), protein, or carbohydrates and protein.

2). Against this spatial variation, mean ant density was 36% higher on +CHO plots (two-tailed $p = 0.055$). Density failed to increase on +Protein plots ($p = 0.630$), a pattern consistent with or without added CHOs (interaction $p = 0.821$).

There was no evidence of changes in species richness with food additions (Table 1), but species composition was altered on the +CHO plots. While the spatial block varied from a least squares mean of 5–16 species/0.25 m^2 ($p < 0.0001$), species richness on plots was uniform across +CHO and +Protein treatments (CHO, Protein and interactions: $p > 0.380$). A Permanova contrasting worker density of the six species found on at least 50% of the plots revealed significant variation across plots (block $F_{28,84} = 1.94$, $p = 0.0002$) and a significant pairwise difference between Control and +CHO plots ($t_{1,84} = 1.5$, $p = 0.030$) but not +Protein ($p = 0.450$) or +CHO + Protein plots ($p = 0.140$). Three myrmicine ants, *Wasmannia auropunctata*, *Solenopsis* JTSp1, and *Cyphomyrmex rimosus*, showed the largest proportional increase from H_2O to CHO plots (Fig. 3).

Traits: tempo, trophic level, and %N

Consistent with a corollary of Economics Hypothesis—the Metabolic Fuel Hypothesis—we found that ant community tempo increased on +CHO but not +Protein plots. After 30 days, neutral platforms (wooden tongue depressors) accumulated four-fold more small ants and three-fold more large ants on +CHO plots (p's < 0.0001, Fig. 4, Table 2); this effect reflects a change in behavior rather than simply a change in ant density, which was included as a covariate in the analysis (p's > 0.300). There was no significant increase of tempo on +Protein plots for either size category of ants (p's > 0.200). In addition, for small ants there was strong spatial variation in activity (block effect $p = 0.002$) and an interaction between +CHO and +Protein treatments for small ants ($p = 0.054$) suggesting that ant activity decreased when CHO and Protein was presented together. Such spatial heterogeneity and treatment interactions were not found in the activity of large ants.

We generated data on whole ant %N for 50 species representing 99% (15345 of the 15514) of sampled ants, and stable isotope $\delta^{15}N$ for 40 species (Appendix B). Whole body N varied from 7.7% in *Solenopsis terricola* to 14.2% in *Anochetus diegensis*. The assemblage spanned two trophic levels (given the 3.4 criteria for $\delta^{15}N$) from 3.4 for *Pyramica subedentata* to 8.6 for *Gnamptogenys horni*. The two traits were unrelated: a species' percentage of whole body N failed to covary

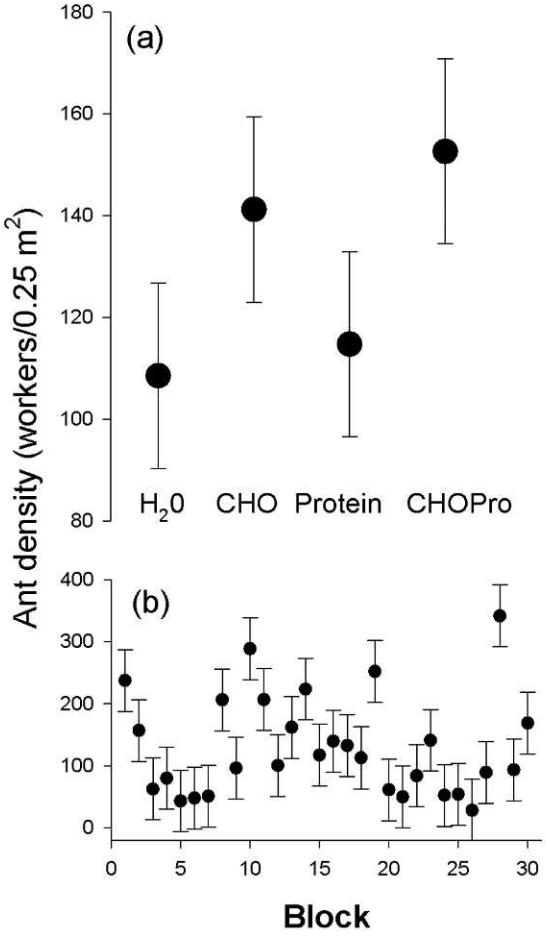

Fig. 2. The density (least square means ± 1 SE) of tropical litter ants varied with food addition (a) and spatially across 30 blocks (b).

with δ^{15}N ($r_{40} = 0.05$, $p > 0.74$).

Consistent with the Economics Hypothesis, adding CHOs to a plot attracted ants with a lower trophic signature (note this didn't result from feeding on CHOs, as species specific δ^{15}N values were generated from ants collected on control plots). When we characterized each plot by the δ^{15}N of its species, weighted by worker density, δ^{15}N marginally decreased by 10% on +CHO plots treatment ($p = 0.054$); but not on +Protein plots ($p = 0.53$) with a possible interaction ($p = 0.093$, Fig. 5, Table 3).

The response of average whole body %N to food supplements was more complex (Fig. 6, Table 3). Although average %N failed to vary with +CHO or +Protein treatments ($p > 0.44$), the interaction term was significant ($p = 0.042$), suggesting a 4–5% increase in average %N on the +CHO and +Protein treatments, but a drop relative to the control when both CHO and Protein were presented together.

Discussion

In a community of 77 sampled ant species, we used a large-scale experiment to test two core hypotheses from nutritional ecology. The Compensation Hypothesis emphasizes the common requirements of consumers, and predicts limitation by the rarest shared nutrient; the Economics Hypothesis emphasizes the stoichiometric basis for niche differences, and predicts changes in composition and behavior based on the balance of available resources. The ant community responded to carbohydrates (CHOs), but not Protein additions in ways consistent with both hypotheses.

The Compensation Hypothesis—an offshoot of Leibig's Law of the Minimum—predicted an important community-level metric: food uptake. In the dark understory of a tropical forest, microbial production via litter decomposition provides a food base with a C:N ratio of 9:1, compared to a green food web's CHO-rich 40:1 (Kaspari and Yanoviak 2001, Sterner and Elser

Table 1. Ant density and species richness on a factorial addition of carbohydrate (CHO) and Protein across 30 blocks.

Source	df	Density			Species richness		
		Type III SS	*F*	pr > *F*	Type III SS	*F*	pr > *F*
CHO	1	373382	3.76	0.056	6.08	0.68	0.412
Protein	1	2323	0.23	0.630	7.00	0.79	0.378
CHO × Protein	1	202	0.02	0.887	6.08	0.68	0.411
Block	29	755020	2.62	0.0003	26.92	3.02	0.0001
Error	87	1658978			776.90		

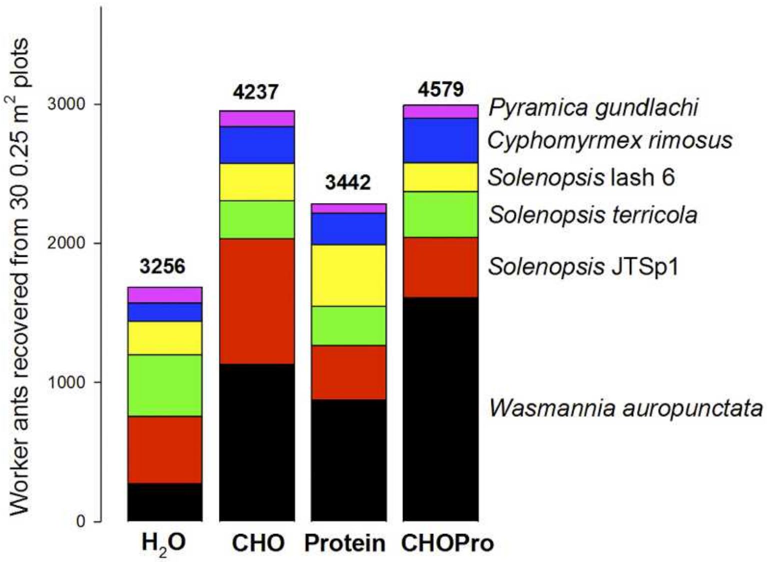

Fig. 3. The composition of plots supplemented with water, sugar, protein, or both, reflected by the six species found on at least half the plots sampled. Numbers above each stacked bar represent total number of ants extracted from that treatment.

2002). Over the course of the experiment, ants used CHO baits at levels consistently higher than controls (Fig. 1) and when extracted from the litter two days following the last baiting, were 36% more abundant on +CHO plots. In contrast, +Protein plots did not differ in ant foraging activity or density. This suggests that the increased abundance of litter ants on plots supplemented with insect necromass (McGlynn 2006, Shik and Kaspari 2010) resulted from a craving for CHOs, and that the scarce natural CHO subsidies to litter environments (via fruit fall, nectar, and insect honeydew) may play an underappreciated role in structuring these com-

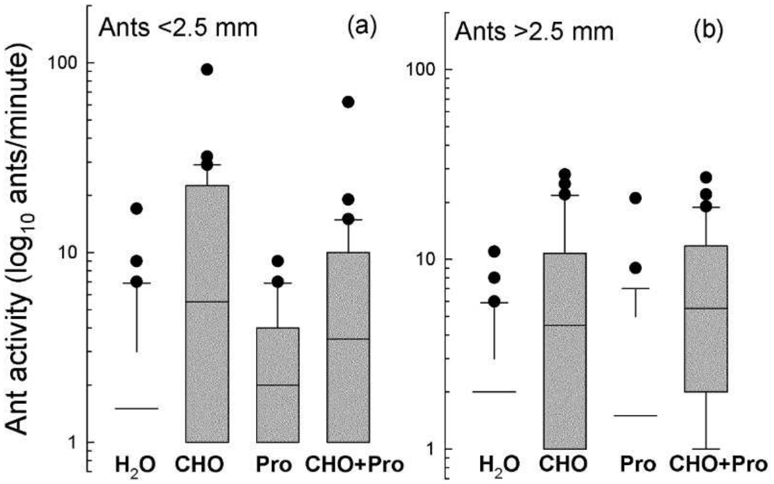

Fig. 4. Activity of small (a) and large (b) litter ants on neutral substrates following 30 days of adding water, carbohydrates, protein, or carbohydrates and protein. The shaded box represents the 25 and 75% quartiles, with the line representing the median value; error bars represent the 10th and 90th percentiles; dots are outliers.

Table 2. Worker activity on neutral substrates as a function of factorial addition of carbohydrate (CHO) and Protein across 30 blocks with worker density as a covariate.

		Ants <2.5 mm			Ants >2.5 mm		
Source	df	Type III SS	*F*	pr > *F*	Type III SS	*F*	pr > *F*
CHO	1	2.91	21.1	<0.0001	3.09	21.1	<0.0001
Protein	1	0.02	0.1	0.732	0.23	1.6	0.213
CHO × Protein	1	0.53	3.8	0.054	0.07	0.5	0.487
$\log_{10}$(no. workers)	1	0.02	0.2	0.685	0.16	1.1	0.303
Block	29	9.08	2.3	0.002	5.05	1.2	0.265
Error	117	11.57			21.20		

munities. If so, the rates of these subsidies to litter ant communities should play a leading role in their regulation, alongside other factors like litter depth, nest site availability, disturbance, and litter mineral content (Kaspari 1996, McGlynn 2006). Moreover, the Compensation hypothesis predicts that a similar experiment, performed in a forest canopy or an old field—habitats with plant exudates—would yield the opposite result (Davidson 1997, Yanoviak and Kaspari 2000). More refined predictions will emerge with development of techniques for quantifying nutrient availability ratios for ant communities; direct measurements of nutrient availability is generally impractical (Tennant and Porter 1991) and indirect techniques using bait visitation (Yanoviak and Kaspari 2000, Kay 2002) likely provide only coarse estimates.

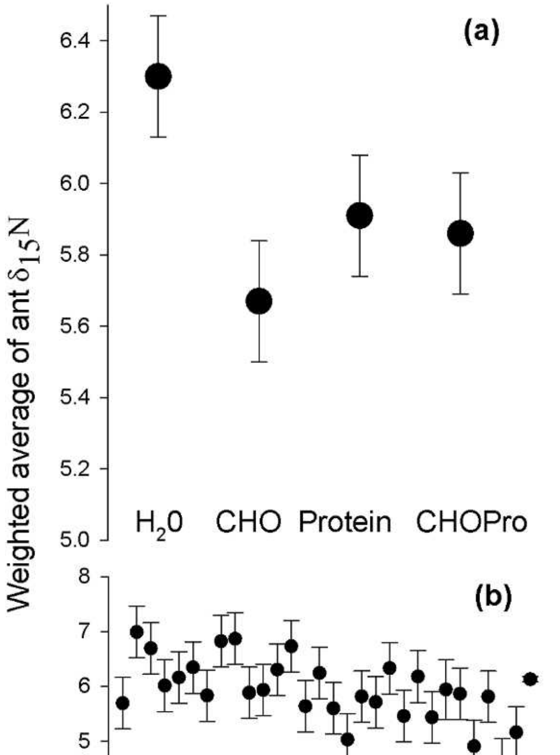

Fig. 5. The average trophic level of ants (least square means ± 1 SE) varied with food addition (a) and spatially across 30 blocks (b).

The Economics Hypothesis, which assumes species differ in functional traits and that those traits have a stoichiometric recipe, predicted the increased activity, or tempo, on +CHO plots (Fig. 4) but not +Protein plots. This Metabolic Fuel Hypothesis (Davidson 1997, Kay et al. 2010) argues that ant activity runs on sugar, and is the basis for high abundance of ants in the N-starved canopy (Davidson et al. 2003) and the prevalence of nectaries in ant-plant symbioses (Ness et al. 2009). The ten-fold increase in ant activity over H_2O plots in the litter is remarkable; suggesting that nutrient limitation can be a significant damper on invertebrate behavior (and in the ecosystem processes they regulate, see also Kaspari et al. 2009). Again, a similar experiment in the tropical canopy, where tempo is already high (Yanoviak and Kaspari 2000) would be of considerable interest.

The Economics Hypothesis also predicted the increased abundance of ants from lower trophic levels on +CHO plots (that is, those preferring a higher proportion of CHOs in their diets). The 10% drop in δ^{15}N likely arose from the accumulation of *Wasmannia* ($\delta^{15}N = 4.4$) and *Cyphomyr-*

Table 3. Ant trophic level and %N for the average worker ant sampled from plots subject to a factorial additions of carbohydrate (CHO) and Protein across 30 blocks.

		Delta$_{15}$ N			% whole body N		
Source	df	Type III SS	F	pr > F	Type III SS	F	pr > F
CHO	1	3.38	3.82	0.054	0.44	0.59	0.443
Protein	1	0.35	0.40	0.530	0.07	0.09	0.764
CHO × Protein	1	2.54	2.88	0.093	3.18	4.28	0.042
Block	29	39.41	1.54	0.066	63.62	2.95	0.0001
Error	86	121.81			131.4		

mex (3.8) relative to the more predacious *Solenopsis* species (JTsp1: 7.4, Lash6: 8.2, *terricola*: 6.4). This decrease approached statistical significance ($p = 0.054$), which could reflect the coarse description of trophic status given by δ^{15}N and the importance of other species traits that affected response to supplementation.

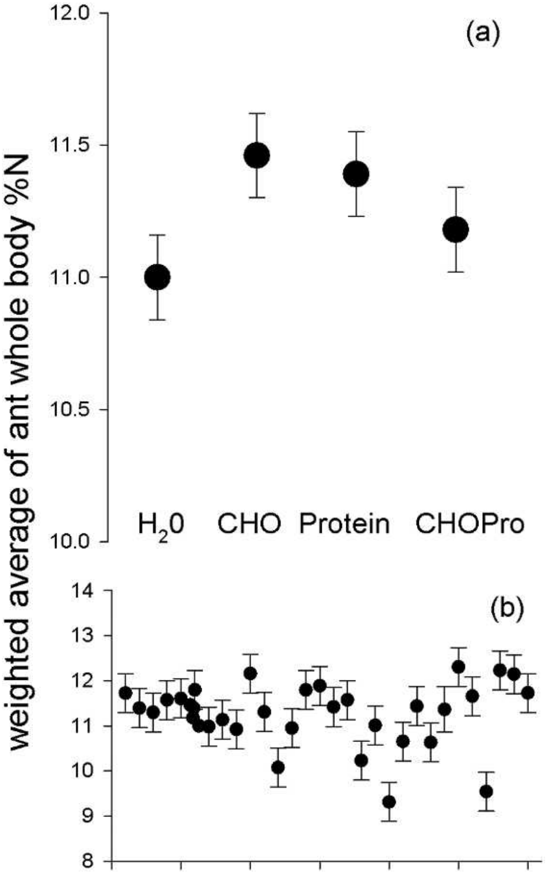

Fig. 6. The average percentage of whole body N of ants (least square means ± 1 SE) varied with food addition (a) and spatially across 30 blocks (b).

Tradeoffs are a key element of the Economics hypothesis. However, we found little evidence from this community that ant species feeding high trophically, and thus enjoying a high-protein diet, have higher %N content ($r = 0.05$). For example, among the six most widespread species, the two most herbivorous taxa (δ^{15}N < 4.4, *Wasmannia* and *Cyphomyrmex*) have among the highest %N, and the genus *Solenopsis*, with uniformly high trophic level (δ^{15}N > 7.3) have %N ranging from 7.7 (*terricola*) to 12.1 (Lash 6). The orthogonality of these two traits was unexpected, and suggests a broad niche space in this community generated by different combinations of %N from herbivores to top predators.

Also, to our surprise, we found little evidence of interaction between CHO and Protein. One scenario—that of a synergy where the quality of plots fueled with CHOs increased when they were also supplemented with Protein—failed. Instead, where there was evidence for CHO-Protein interaction, Protein ameliorated the CHO induced increase in ant activity (Fig. 4), decrease in average trophic level, and the increase in average %N (Fig. 5). Higher dietary Protein:CHO can lead to reduced performance and higher mortality in both solitary (Lee et al. 2008, Makalkov et al. 2008) and social (Dussutour and Simpson 2009, Kay et al. 2012) insects, presumably because of costs associated with eliminating nitrogenous waste products (Lee et al. 2008, Kay et al. 2012). Further work is needed to determine if such individual level performance costs can lead to community-level patterns like those we observed in this study.

Caveats

There are a few caveats to consider when interpreting these results. We used number of feeding ants to estimate food uptake; this measure can differ significantly from consumption rates (Cook and Behmer 2011). Baits were occasionally fed upon by other arthropods (dung beetles, crickets, opiliones) that could impact ant communities, but these feeding events were very rare (<0.5% of bait observations).

Based on F values, CHO availability accounted for far less variation than block in accounting for activity and abundance. Spatial variation in unmeasured ecological factors likely had important effects on our results: although our block design allowed us to control for some of this variation, litter depth, disturbance, predation, and other important factors can show fine-scale variation in this system. It is interesting to speculate how a longer-term experiment may have increased the signal of food addition. But the continual shifting litter habitat as trees drop their leaves (Donoso et al. 2010) may make habitat based patchiness a dominant theme regardless of food supply.

Finally, while litter ants are highly mobile and may move their colonies on a weekly schedule (Byrne 1994, McGlynn 2006) it is possible that the dynamics of Protein limitation—underlying as they do larval growth and development—may be inadequately appreciated over the 4–8 weeks of this study. If so, a longer-term experiment would have revealed changes in density reflected by higher colony growth rates. Such experiments could also reveal density dependent changes in the observed increases in activity and density on +CHO plots, associated with depletion of prey or accumulation of parasites.

CONCLUSION

The use of nutritional ecology to generate patterns in consumer communities is still in its infancy. Studies of the direct and indirect effects of distinct resources have been fundamental to plant ecology theory on niche differentiation (Tilman 1986), productivity-diversity relationships (Rosenzweig and Abramsky 1993) and the distributions of functional traits (Behmer 2008, Raubenheimer et al. 2009). Recent work in nutritional ecology demonstrating the importance of nutrient balance on animal performance (Behmer 2008, Raubenheimer et al. 2009) suggests that nutritionally explicit work in animal communities may improve understanding of how bottom-up forces structure consumer communities (Simpson et al. 2010). Our work indicates that litter ants are a tractable system for such work. At the same time, studies of the many other taxa of the brown food web, including the microbes now known to be limited by a variety of nutrients (van Groenigen et al. 2006, Kaspari et al. 2008), would profit from the framework of nutritional ecology.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Total berlese capture and proportion (of 15,514 ants collected) of ant species recorded from berlese extractions. Species names bracketed by "_" are morphospecies.

Subfamily	Genus	Species	Total	Proportion
Formicinae	*Acropyga*	*exsanguis*	1	0.01
Ponerinae	*Anochetus*	*diegensis*	27	0.17
Myrmicinae	*Apterostigma*	*auriculatum*	1	0.01
Myrmicinae	*Basiceros*	*manni*	1	0.01
Formicinae	*Camponotus*	*_antcnp_sp1_*	1	0.01
Myrmicinae	*Carebara*	*reina*	7	0.05
Myrmicinae	*Carebara*	*urichi*	3	0.02
Myrmicinae	*Cephalotes*	*atratus*	1	0.01
Myrmicinae	*Crematogaster*	*sumichrasti*	1	0.01
Myrmicinae	*Cyphomyrmex*	*costatus*	189	1.22
Myrmicinae	*Cyphomyrmex*	*rimosus*	946	6.1
Ponerinae	*Discothyrea*	*humilis*	22	0.14
Dolichoderinae	*Dolichoderus*	*bispinosus*	10	0.06
Ectatomminae	*Ectatomma*	*ruidum*	75	0.48
Ectatomminae	*Gnamptogenys*	*hartmani*	1	0.01
Ectatomminae	*Gnamptogenys*	*horni*	39	0.25
Ectatomminae	*Gnamptogenys*	*minuta*	6	0.04
Ectatomminae	*Gnamptogenys*	*triangularis*	4	0.03
Ponerinae	*Hypoponera*	*_JTL007_*	64	0.41
Ponerinae	*Hypoponera*	*_JTL013_*	57	0.37
Ponerinae	*Hypoponera*	*_sp2_*	25	0.16
Ponerinae	*Hypoponera*	*distinguenda*	8	0.05
Ponerinae	*Hypoponera*	*parva*	32	0.21
Myrmicinae	*Megalomyrmex*	*mondaboroides*	1	0.01
Myrmicinae	*Megalomyrmex*	*silvestrii*	104	0.67
Myrmicinae	*Monomorium*	*pharaonis*	2	0.01
Myrmicinae	*Myrmicocrypta*	*_mek01_*	4	0.03
Formicinae	*Nylanderia*	*guatamalensis*	586	3.78
Myrmicinae	*Octostruma*	*balzani*	302	1.95
Ponerinae	*Odontomachus*	*bauri*	48	0.31
Ponerinae	*Pachycondyla*	*arhuaca*	4	0.03
Ponerinae	*Pachycondyla*	*constricta*	3	0.02
Ponerinae	*Pachycondyla*	*harpax*	42	0.27
Ponerinae	*Pachycondyla*	*impressa*	1	0.01
Formicinae	*Paratrechina*	*longicornis*	2	0.01
Myrmicinae	*Pheidole*	*_21YB_*	2	0.01
Myrmicinae	*Pheidole*	*_lash9_*	224	1.44
Myrmicinae	*Pheidole*	*angulifera*	5	0.03
Myrmicinae	*Pheidole*	*dasypyx*	12	0.08
Myrmicinae	*Pheidole*	*fimbriata*	1	0.01
Myrmicinae	*Pheidole*	*harrisonfordi*	275	1.77
Myrmicinae	*Pheidole*	*mendicula*	112	0.72
Myrmicinae	*Pheidole*	*multispina*	182	1.17
Myrmicinae	*Pheidole*	*psilogaster*	1	0.01
Myrmicinae	*Pheidole*	*rugiceps*	200	1.29
Myrmicinae	*Pheidole*	*sensitiva*	1	0.01
Myrmicinae	*Pheidole*	*zeteki*	123	0.79
Pseudomyr-mecinae	*Pseudomyrmex*	*oculatus*	2	0.01
Myrmicinae	*Pyramica*	*_horse_*	1	0.01
Myrmicinae	*Pyramica*	*_mek1_*	8	0.05
Myrmicinae	*Pyramica*	*brevicornis*	102	0.66
Myrmicinae	*Pyramica*	*gundlachi*	383	2.47
Myrmicinae	*Pyramica*	*subedentata*	61	0.39
Myrmicinae	*Pyramica*	*zeteki*	98	0.63
Myrmicinae	*Rogeria*	*_antcnp_sp2_*	12	0.08
Myrmicinae	*Rogeria*	*creightoni*	40	0.26
Myrmicinae	*Rogeria*	*foreli*	17	0.11
Myrmicinae	*Sericomyrmex*	*amabilis*	7	0.05

Table A1. Continued.

Subfamily	Genus	Species	Total	Proportion
Myrmicinae	*Sericomyrmex*	*urichi*	2	0.01
Myrmicinae	*Solenopsis*	*_JT_sp1_*	2213	14.26
Myrmicinae	*Solenopsis*	*_lash1_*	10	0.06
Myrmicinae	*Solenopsis*	*_lash4_*	1363	8.79
Myrmicinae	*Solenopsis*	*_lash6_*	1156	7.45
Myrmicinae	*Solenopsis*	*_sp1_*	17	0.11
Myrmicinae	*Solenopsis*	*_sp2_*	330	2.13
Myrmicinae	*Solenopsis*	*_sp3_*	7	0.05
Myrmicinae	*Solenopsis*	*_yellow_*	649	0.24
Myrmicinae	*Solenopsis*	*subterranea*	31	0.2
Myrmicinae	*Solenopsis*	*terricola*	1327	8.55
Myrmicinae	*Strumigenys*	*elongata*	7	0.05
Myrmicinae	*Strumigenys*	*lanuginosa*	8	0.05
Myrmicinae	*Strumigenys*	*marginiventris*	5	0.03
Ponerinae	*Thaumatomyrmex*	*_sp2_*	2	0.01
Ponerinae	*Thaumatomyrmex*	*atrox*	3	0.02
Myrmicinae	*Trachymyrmex*	*cornetzi*	2	0.01
Myrmicinae	*Trachymyrmex*	*zeteki*	1	0.01
Myrmicinae	*Wasmannia*	*auropunctata*	3889	25.07

APPENDIX B

Table B1. Traits of 50 of 77 ant species (99% of berlese captures). Species names bracketed by "_" are morphospecies. Each species characterized by total berlese capture, number of samples, and the percent nitrogen of worker ants, and the stable isotope value for nitrogen.

Subfamily	Genus	Species	Total	*n*	%N	δN
Myrmicinae	*Wasmannia*	*auropunctata*	3889	9	12.4	4.4
Myrmicinae	*Solenopsis*	*_JTsp1_*	2213	4	9.8	7.4
Myrmicinae	*Solenopsis*	*_lash4_*	1363	6	10.7	7.3
Myrmicinae	*Solenopsis*	*terricola*	1327	1	7.7	6.5
Myrmicinae	*Solenopsis*	*_lash6_*	1156	2	12.1	8.2
Myrmicinae	*Cyphomyrmex*	*rimosus*	946	9	11.7	3.8
Myrmicinae	*Solenopsis*	*_yellow_*	649	3	10.4	6.7
Formicinae	*Nylanderia*	*guatamalensis*	586	10	10.6	4.5
Myrmicinae	*Pyramica*	*gundlachi*	383	2	11.5	7.5
Myrmicinae	*Solenopsis*	*_sp2_*	330	5	10.8	.
Myrmicinae	*Octostruma*	*balzani*	302	6	12.2	7.5
Myrmicinae	*Pheidole*	*harrisonfordi*	275	13	11.8	6.2
Myrmicinae	*Pheidole*	*_lash9_*	224	6	12.2	5.5
Myrmicinae	*Pheidole*	*rugiceps*	200	14	11.8	5.1
Myrmicinae	*Cyphomyrmex*	*costatus*	189	5	11.9	5.5
Myrmicinae	*Pheidole*	*multispina*	182	11	11.2	
Myrmicinae	*Pheidole*	*zeteki*	123	2	13.9	4.2
Myrmicinae	*Pheidole*	*mendicula*	112	9	10.0	7.6
Myrmicinae	*Megalomyrmex*	*silvestrii*	104	5	10.0	3.8
Myrmicinae	*Pyramica*	*brevicornis*	102	2	10.9	6.8
Myrmicinae	*Pyramica*	*zeteki*	98	7	12.0	3.4
Ectatomminae	*Ectatomma*	*ruidum*	75	3	13.9	7.5
Ponerinae	*Hypoponera*	*_JTL007_*	64	4	12.1	6.2
Myrmicinae	*Pyramica*	*subedentata*	61	1	13.2	3.4
Ponerinae	*Odontomachus*	*bauri*	48	5	13.6	6.0
Ponerinae	*Hypoponera*	*_JTL013_*	45	5	13.6	7.1
Ponerinae	*Pachycondyla*	*harpax*	42	6	12.2	7.6
Myrmicinae	*Rogeria*	*creightoni*	40	2	13.8	6.9
Ectatomminae	*Gnamptogenys*	*horni*	39	6	14.2	8.6
Ponerinae	*Hypoponera*	*_sp2_*	33	2	13.6	7.6
Ponerinae	*Hypoponera*	*parva*	32	5	13.7	7.8
Ponerinae	*Anochetus*	*diegensis*	27	3	14.2	7.2
Myrmicinae	*Rogeria*	*foreli*	17	1	13.6	6.7

Table B1. Continued.

Subfamily	Genus	Species	Total	*n*	%N	δN
Myrmicinae	*Pheidole*	*dasypyx*	12	8	11.9	6.1
Dolichoderinae	*Dolichoderus*	*bispinosus*	10	5	11.5	
Myrmicinae	*Pyramica*	*_mek1_*	8	1	13.2	6.1
Myrmicinae	*Sericomyrmex*	*amabilis*	7	3	12.6	2.0
Myrmicinae	*Strumigenys*	*marginiventris*	5	1	13.5	5.4
Ponerinae	*Pachycondyla*	*arhuaca*	4	3	10.1	7.0
Myrmicinae	*Myrmicocrypta*	*_mek01_*	4	1	12.1	3.7
Myrmicinae	*Carebara*	*urichi*	3	1	14.1	5.3
Ponerinae	*Pachycondyla*	*constricta*	3	2	13.7	4.9
Ponerinae	*Thaumatomyrmex*	*atrox*	3	1	13.7	5.0
Myrmicinae	*Monomorium*	*pharaonis*	2	5	10.3	
Formicinae	*Paratrechina*	*longicornis*	2	1	11.6	
Pseudomyrmec	*Pseudomyrmex*	*oculatus*	2	11	9.9	
Formicinae	*Camponotus*	*_antcnp_sp1_*	1	10	9.5	
Myrmicinae	*Crematogaster*	*sumichrasti*	1	3	11.3	
Ponerinae	*Pachycondyla*	*impressa*	1	1	13.0	
Myrmicinae	*Apterostigma*	*auriculatum*	1	1	12.1	6.5