Litter Biomass and Nutrient Determinants of Ant Density, Nest Size, and Growth in a Costa Rican Tropical Wet Forest

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ABSTRACT

The nutritional demands of animals vary by taxon. Across landscapes, communities of animals experience variability in the stoichiometry of carbon and nutrients within their resource base. Thus, we expect stoichiometry to contribute to the spatial variance in the demographic parameters of animal communities. Here, we measure how the composition of a litter-nesting tropical rainforest ant community is influenced by spatial variation in environmental stoichiometry relative to litter biomass, a known predictor of ant density. We found the density of ants and their nests were strongly related to litter biomass and carbon: phosphorus stoichiometry. The spatial variation in soil nutrients, which determines leaf litter stoichiometry, was an excellent predictor of nest size in the two most common genera of ants. We found a negative relationship between species' growth rate and local soil stocks of phosphorus. Overall, the density of litter-dwelling ants varied greatly across this tropical forest landscape and environmental stoichiometry can account for limits on ant density independent of the biomass of the leaf litter resource base.

Key words: ants; detritus; ecological stoichiometry; *Pheidole*; phosphorus; *Pyramica*; *Solenopsis*.

ECOLOGISTS HAVE LONG SOUGHT UNIVERSAL THEORIES FOR COMMUNITY COMPOSITION in the tropics that transcend site-specific differences (Andrewartha & Birch 1954, MacArthur 1969, Connell 1978, Hubbell 2001). Much of the variance in the composition of animal communities can be explained by the abiotic environment. Such explanations are scale-dependent, and often habitat-specific, because of spatial heterogeneity (Whittaker 2000). At the coarsest spatial scales, climatic parameters explain a substantial portion of the variance in density and richness of a community (Gaston 2000, Kaspari *et al.* 2000). While the mechanisms driving large-scale patterns in biodiversity are debatable, ecologists agree that the abiotic aspects of climate are the most significant ultimate drivers of biodiversity at continental scales (Currie *et al.* 2004). At the finest spatial scales, microclimate and microhabitat can explain patterns of density, and potentially body size, in terms of habitat selection (Clémencet & Doums 2007). For example, litter-dwelling organisms in tropical rainforests will occur in higher densities where there is greater biomass of leaf litter on the forest floor (Kaspari 1996, McGlynn *et al.* 2007).

Whereas microhabitat and climate account for animal density at the extremes of spatial scale, determinants of community composition at the mesoscale are poorly known, particularly in terrestrial animal communities (Andersen 1997, Fraser 1998, Gotelli & Ellison 2002). The literature is replete with examples wherein

climate, microclimate, and microhabitat partially account for mesoscale variation in biodiversity, over the range of a few kilometers to a few hundred kilometers (Hutchings *et al.* 2003). Environmental regulation of animal density and growth at the mesoscale is best known from aquatic and marine systems (Moe *et al.* 2005). In these environments, limitation by macronutrients and micronutrients is a principal determinant of density and growth. The cycling of nutrients in terrestrial ecosystems is far slower than in aquatic systems. Consequently, spatial heterogeneity in nutrient distributions might be responsible for mesoscale variation in density (Jones *et al.* 2006).

At fine spatial grains, limiting nutrients may drive properties of animal communities that covary with stoichiometric gradients (Milton & Kaspari 2007). The abundance of a single element may show associations with community properties; however, within organismal tissues, groups of elements often demonstrate multivariate elemental signatures associated with particular biological functions (Sterner & Elser 2002). To evaluate competing mechanisms that may account for community responses to resource stoichiometry, we must first understand the associations that occur; this is a research priority in detrital food webs (Moore *et al.* 2004). This approach is particularly important in the leaf litter of tropical rainforests, where no single nutrient limits all processes (Kaspari *et al.* 2008).

Multiple mechanisms may describe how communities respond to resource stoichiometry (Sterner & Elser 2002). The threshold element ratio hypothesis suggests that the availability of one or more limiting elements—often nitrogen (N) or phosphorus (P)—may ultimately limit primary productivity, driving the density

of arthropods through classic bottom-up control (Ritchie 2000, Maraun *et al.* 2001, Sterner & Elser 2002, Frost & Elser 2002, McGlynn *et al.* 2007). In environments with primary consumers that are highly calcareous relative to their food supply, such as oribatid mites, calcium (Ca) may also be limiting (Reichle *et al.* 1969, Norton & Behan-Pelletier 1991). The growth rate hypothesis predicts that under P limitation, consumer tissue production is constrained because ribosomal RNA is P-rich (Elser *et al.* 2000, Schade *et al.* 2003). More generally, Sterner and Elser (2002) predicted that faster growing species will occur in high-nutrient sites, which we refer to as the fertility–growth association hypothesis. If a toxic metal such as aluminum (Al) or manganese (Mn) is in particularly high concentrations, animal growth or density may be decreased (Tabak & Gibbs 1991, Delhaize & Ryan 1995, Behmer *et al.* 2005); we refer to this as the toxic element hypothesis. More generally, relatively rare micronutrients such as molybdenum (Mo) or selenium (Se) may also limit or accelerate the process of litter decomposition (Kaspari *et al.* 2008).

Moe *et al.* (2005) recommended investigation of terrestrial insects and detrital food webs as the most fruitful avenues in stoichiometry and community ecology. We find several advantages in focusing on ants nesting within detritus. This guild is ecologically dominant, species rich, and trophically diverse (Hölldobler & Wilson 1990). Diverse ant communities demonstrate high sensitivity to environmental gradients (Andersen & Majer 2004). Entire nests of litter-dwelling ants may be collected as a single ecological unit, with growth rates estimated using the relative proportions of individuals representing the pupal and adult developmental stages (Wilson 1971). Unlike many other invertebrate taxa in detrital food webs, all individual ants can be readily and reliably sorted to species.

The density of litter-dwelling ants increases with litter biomass, which serves as habitat and as the foundation of the food web supplying ants with prey. Because the biomass of litter can only account for a fraction of the variance in ant densities, we may expect additional variation to be explained by resource stoichiometry. We are only starting to describe regional gradients in environmental stoichiometry (Reich 2005). According to reviews (Sterner & Elser 2002, Moe *et al.* 2005), no prior study has evaluated the relationships between environmental stoichiometry and the composition of a terrestrial animal community. Here, we test whether spatial heterogeneity in nutrient availability can account for variance in ant density, nest size, and growth rates across a tropical rain forest landscape, in a site where soil P predicts the density of the litter arthropod fauna (McGlynn *et al.* 2007). Across this site, soil stoichiometry is spatially coupled with the stoichiometry of leaf litter (Wood *et al.* 2006), the resource base of ants supported by the detrital food web. We evaluate associations among litter biomass, local soil nutrients, and the litter ant community in the context of the above-described hypotheses: Fertility–growth association, growth rate, threshold element, and toxic element. The discovery of such associations may narrow the picture for the contextualization of future experiments to explain how spatial variation higher up in the food chain may be caused by spatial variation in resource stoichiometry.

METHODS

Our study was a located in lowland tropical rain forest at the La Selva Biological Station, Costa Rica ($10°26'$ N, $84°00'$ W; 37–150 m asl, mean annual rainfall 4 m; www.ots.ac.cr/en/laselva). In May–June 2004, we sampled the litter-nesting ant fauna at eighteen 0.5-ha plots set out in a stratified-block design across the major edaphic gradients (slope, soil type) of a *ca* 500-ha old-growth forest landscape. Inter-plot distances ranged to multiple kilometers (the CARBONO Project plots; Clark & Clark 2000). We used a standardized intensive sampling protocol (McGlynn 2006). We removed all fine litter (leaf and reproductive material, twigs < 1 cm diameter) from ten 1-m^2 quadrats spaced at 10-m intervals in a linear transect along the length of each plot; for slope plots, samples of ants and soils were taken from the ridgetop to minimize variance in edaphic properties. Within 12 h after collection, the litter was searched exhaustively for all ant nests; the ant samples were stored in 95 percent ethyl alcohol until analysis. We define a nest as a group of conspecific ants containing adults and brood and cohabiting a single structural element of the leaf litter, such as a twig, curled-up leaf, or seedpod. Between September 2004 and June 2006, all ants were identified to species or morphospecies using identification tools available at www.evergreen.edu/ants (authored by J.T. Longino). The contents of the nests were counted, including all castes of pupae and adults.

Soil chemistry was determined for each plot based on compositing six regularly spaced soil cores (0–10 cm depth) inside the 50 × 100 m plot. After being air-dried, sieved (2 mm) and ground, the samples were analyzed at the Institute of Soil Science and Forest Nutrition, University of Göttingen, Germany (see Veldkamp *et al.* 2003). Total carbon (C) and total N were analyzed with a CHN analyzer and total P by HNO$_3$-pressure extraction and ICP-AES (Inductively Coupled Plasma Atomic Emission Spectroscopy); indices of available P have been found to be poorly related to ecosystem function at this site (*cf.*, Powers *et al.* 2005). Soil stocks of C, P, and N were calculated from mean concentrations, adjusted by mean values for bulk density on each soil type, and were expressed as molar ratios (C: N, C: P). Concentrations of Al, Ca, iron (Fe), potassium (K), magnesium (Mg), and Mn were measured with a Varian SpectrAA ® Atomic Absorption Spectrometer using 1M NH$_4$Cl percolation.

Six mo prior to ant sampling, in each of the 18 plots, fine litterfall was collected every 2 wk in nine evenly spaced pairs of 0.25-m^2 litter traps, one a mesh bag 0.8 m above the ground, the other a ground-level quadrat from which the larger leaf litter items (> 50 cm) were collected. The collected litter was separated by component (leaves, twigs < 1 cm diameter, reproductive litter such as flowers and fruits) and dried to constant mass at 65°C. The nutrient content of these plot-level litter samples was assayed over a time series; soil C: N: P stoichiometry was shown to serve as an excellent time-integrated indicator of litter stoichiometry at the plot level (Wood *et al.* 2005).

To estimate the biomass of standing fine litter (leaves + reproductive litter + twigs < 1 cm diameter) on the forest floor at the time of ant sampling, the litter collected from each 1-m^2 plot was weighed for fresh mass, and a representative subsample was dried

to constant mass at 65°C (the entire sample volumes were too large to process in toto). The density of litter-dwelling detritivores (potential prey of ants such as collembola and mites) at each site was obtained from McGlynn *et al.* (2007). The density of workers was calculated using mean adult workers/m^2.

Analyses were performed with PISTE (Vaudor, A., 2000, English version 3.1.2, Univ. of Montreal, Canada) and JMP 5.1.2 (SAS Institute 2004, Cary, NC). We developed an *a priori* path model incorporating known and hypothesized relationships among litter biomass, nutrients, and faunal densities (Kaspari 1996, Moore *et al.* 2004, Wood *et al.* 2006, McGlynn *et al.* 2007). We structured the path model to evaluate the relative influence of biomass inputs and the nutrients associated with the toxic element and threshold element hypotheses.

Demographic measures of ants must additionally take into account their social biology, as nests function as ecological units. We evaluated nest density (nests/m^2) and nest size (adult workers/nest). We separately evaluated mean nest density and mean nest size for the three most abundant litter-nesting genera (*Pheidole, Solenopsis,* and *Pyramica*), as well as all of the remaining genera pooled together. To ensure adequate characterization of a taxon in each site, in this analysis we excluded any data for a taxon from a site if the taxon was represented by fewer than three nests.

Whereas our functional hypotheses related to total ant densities were evaluated by path modeling, there was scant *a priori* basis for modeling nest density and size. Instead, we employed a model selection approach using best subsets multiple regression (BSR) to identify the model with the lowest mean square error (MSE), to a maximum of three variables. The selected models were used to conduct multiple regression for analysis. These analyses were conducted independently for each genus in an attempt to account for differences in life history related to nest size.

To estimate nest growth, we divided the size of the future workforce (number of worker pupae) by the size of the existing workforce (number of worker adults). This indicator can be used to compare nest growth rates across plots and across taxa (Kaspari 1996, McGlynn 2006). This analysis was conducted at the level of the nest, the plot, and within each of the genus-level categories. To evaluate the growth rate hypothesis, predicated on its assumptions being met (as we did not measure RNA P content), we related each growth measure to soil C:P using univariate regression.

To test the fertility–growth association hypothesis, we compared the growth rates of the most common species to the mean soil C:P of the plots where the nests of those species occurred. The seven species in this analysis were those sampled at least 15 times, a reasonable estimate of the number of samples required to be representative of the range in the population (Dytham 2003).

RESULTS

ANT DENSITIES.—The results from the *a priori* path model indicated C:P stoichiometry and leaf litter biomass inputs significantly accounted for variance in ant densities among sites (Fig. 1), with large path coefficients for both litter variables (litterfall rate and standing biomass) as well as C:P stoichiometry.
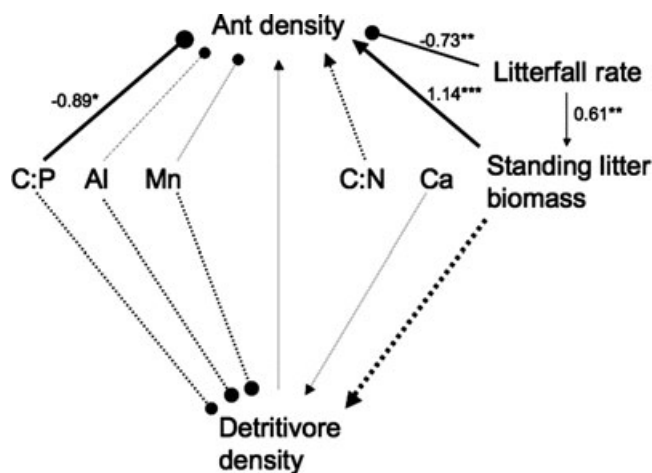

FIGURE 1. *A priori* path model of relationships among biomass inputs, resource stoichiometry, and ant density. Statistically significant paths are indicated with their corresponding path coefficients (* indicates $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Arrows indicate positive associations and terminal circles indicate negative associations. The magnitudes of the connecting lines are associated with the magnitudes of the path coefficient.

NEST DENSITIES.—From the total sample of 180 m^2 of forest floor, we collected 357 entire nests, representing 21 ant genera and 68 species (Table S1). Worker density was well associated with nest density ($R^2 = 0.77$, $F_{1,16} = 54.8$, $P < 0.0001$; $y = 31.3x + 34.9$).

The nest densities of the ant taxa were independent of one another, aside from a positive association between *Pheidole* and *Solenopsis* (Kendall's Tau 0.47; $P = 0.01$). For these two genera, nest density was strongly related to the biomass of standing fine litter (Table 1). Among plots, the mean nest density per m^2 quadrat ranged from 0.6 to 3.6 nests/m^2, with a mean of 2.1/m^2. Much of the variance in the nest density was predicted by the standing fine litter biomass present at the time of sampling ($R^2 = 0.45$, $F_{1,16} = 13.1$, $P < 0.01$). Nest density was not, however, associated with the total fine litterfall inputs over the prior 6 mo ($R^2 = 0.11$, $F_{1,16} = 2.1$, $P = 0.17$).

NEST SIZE.—Nest size varied considerably across plots (plot-level means 16.3–53.8 ants/nest; mean 31.5 ants/nest, SD = 9.2, $N = 18$ plots). Nest size was not associated with the mean fine litter biomass present at a plot ($R^2 < 0.01$); in fact an outlying plot with the greatest litter biomass had the smallest nests. The predictors of nest size varied by taxa (Table 1). The most parsimonious model for *Pheidole* nest sizes identified associations with soil C:P and soil Fe concentrations, whereas the most parsimonious model for *Solenopsis* included soil Fe and soil Mg.

NEST GROWTH.—Pooling all nests per plot, growth rates did not vary with soil C:P. The mean number of pupal workers per adult workers per plot was unrelated to soil C:P at the plot ($R^2 = 0.06$; $F_{1,16} = 1.06$, $P = 0.32$). Similarly, no association with plot soil

TABLE 1.   *Selection of the most parsimonious BSR (best sets regression) for nest density and nest size against litter biomass and nutrient variables. Negative associations are in italics; groups with zero variables did not have significant associations with the models selected for analysis. MSE: mean square error.*

Group		Nest density variable(s)	R^2	MSE	R^2adj.	F_{DF}	P		Nest size variable(s)	R^2	MSE	R^2adj.	F_{DF}	P
Pheidole	1	Log fine litter biomass	0.36	5.06				1	*Soil C:P*	0.39	12.82			
	2	Log fine litter biomass, *soil Ca*	0.42	4.99				2	*Soil C:P*, soil Fe	0.46	12.46	0.39	$6.43_{2,15}$	0.009
	3	Log fine litter biomass, soil Ca, soil Al	0.48	4.88	0.38	$4.37_{3,14}$	0.02							
Pyramica	0							0						
Solenopsis	1	Log fine litter biomass	0.48	2.39				1	Soil Mg	0.40	17.49			
	2	Log fine litter biomass, *soil C:N*	0.65	2.00				2	Soil Mg, *soil Fe*	0.62	14.53			
	3	Log fine litter biomass, soil Ca, soil Al	0.80	1.60	0.75	$18.1_{3,14}$	<0.0001	3	Soil Mg, *soil Fe*, log soil Mn	0.81	10.86	0.75	$13.9_{3,10}$	0.0007
Other genera	1	*Soil C:N*	0.38	1.97				0						
	2	*Soil C:N*, log fine litter biomass	0.48	1.87	0.41	$6.88_{2,15}$	0.008							

C:P was shown by either the mean number of pupal workers per plot ($R^2 = 0.07$; $F_{1,16} = 1.29$, $P = 0.27$) or by the mean number of worker pupae per nest ($R^2 = 0.14$; $F_{1,16} = 2.60$, $P = 0.13$). Among the most common species (the only ones which could be analyzed in this fashion), there was a strong positive relationship between species' mean rates of nest growth and the mean soil C:P at the plots where their nests were collected (Fig. 2).

DISCUSSION

As expected, the densities of ants and their nests were associated with litter biomass. We set out to discover whether additional variance in ant densities were associated with landscape-scale variation in soil stoichiometry. We found that site-specific properties of nutrient limitation also account for the abundance of ants and the sizes of their nests. These correlative relationships may be explained by a multitude of mechanisms, as nutrient concentrations of soil cascade into the tissues of ants through multiple trophic levels. Our results are informative for the hypotheses we set out to evaluate, and we glean some additional insights from the cumulative findings.

The most common litter-nesting ant species in our samples demonstrated differences in growth rates that corresponded with their occurrence along the soil and litter phosphorus gradient in this forest. Competition theories, taking into account differential abilities to exploit high resource environments, might explain this observed pattern (Tilman 1994, Sterner & Elser 2002). Landscape-scale variation in stoichiometry may result in selection for within-guild stoichiometric specialists. However, even the most common ant species in our study cannot yet be assessed in terms of possible differences in diet (Wilson 2005). It is possible that some of these species specialize upon a prey base specific to litter in different stages of decomposition, reflecting shifts in the stoichiometry of the resource base (Moore *et al.* 2004).

We found that ant demographic characteristics vary along the soil and litter C:P gradient in this forest. The sizes of ant nests were predicted by C:P in the most abundant genus, *Pheidole*, even though there was no effect upon the total density of ants per square meter. In other words, C:P does not change the total number of
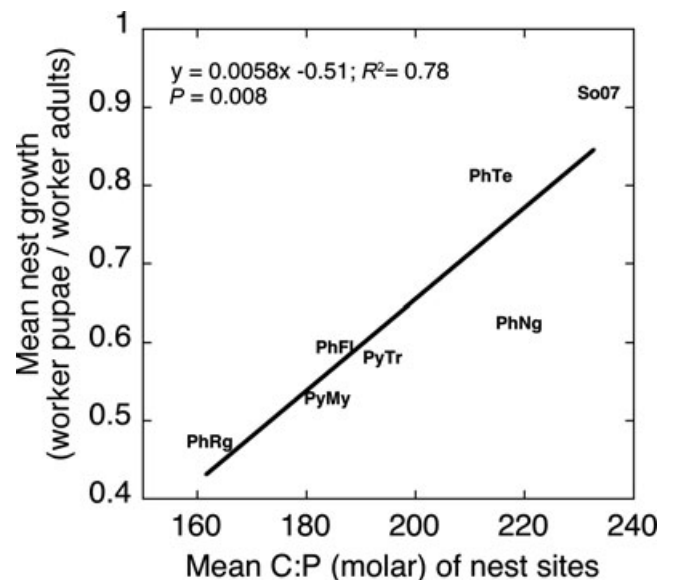

FIGURE 2.   Mean nest growth of the most common species relative to soil C:P at nest sites. Nest growth was measured by dividing the number of pupal workers by the number of adult workers. The mean soil C:P at the nest sites was measured by taking the mean of all of the soil C:P values for the plots where nests of that species were collected. The species abbreviations are as follows: PhFl = *Pheidole flavens*, PhNg = *Pheidole nigricula*, PhRg = *Pheidole rugosus*, PhTe = *Pheidole tennantae*, PyTr = *Pyramica trieces*, PyMy = *Pyramica myllorhapha*, So07 = *Solenopsis* JTL-07.

ants, but C:P altered how these ants are distributed among nests in this one common genus. Viewed simplistically, nest size may be viewed as a long-term integrated measure of nest growth. But the nest size of litter ants must be interpreted in light of their reproductive biology. It is highly likely that the nests of most species reproduce by budding or fission (Byrne 1994, McGlynn 2006). The decision to reproduce a nest by fragmentation is not simple, and probably involves factors such as within-nest conflicts of interest, competition, and the availability of food and nests (Peeters & Ito 2001).

The fact that *Pheidole* nest sizes varied with C:P, but not the total number of ants, indicated that the threshold size triggering the behavioral decision to split a nest apart was greater in high P environments. This is best explained by the increase in the cost of central-place foraging when resource densities are lower (Bernstein 1975). Because the density of ant prey is greater in P-rich sites (McGlynn *et al.* 2007), it is reasonable to expect an associated increase in nest size because the colonies will be less constrained by the inefficiencies of searching for food for longer durations and at greater distances from their nests.

It is generally thought that P limits primary productivity at our research site, as in many other tropical rainforests (Vitousek & Sanford 1986, Powers *et al.* 2005, but see Porder *et al.* 2007). P limitation of faunal productivity may be more widespread than has been generally recognized (Jeyasingh & Weider 2005, Wassen *et al.* 2005). The growth rate hypothesis is a promising mechanistic explanation for the relationship between soil C:P and litter-arthropod densities we have found at this site (McGlynn *et al.* 2007). We expected growth rates of all ants as a single group would be explained by C:P, but our estimate of growth from pooling together all species at the nest and plot levels demonstrated no such association.

We were surprised to find an overt opposite to the prediction of the fertility–growth association hypothesis. The tightness of this relationship suggests that P, or another factor highly correlated with P, is responsible for the distribution of ant species. This relationship is enigmatic, particularly in light of the fact that arthropod densities at La Selva are negatively associated with soil C:P (McGlynn *et al.* 2007). Several non-mutually-exclusive explanations are plausible. Stocks of arthropods do not necessarily correlate with fluxes, and high-density populations might be growing slowly. The decomposition rate of leaf litter may be greater when litter is rich in P (Wood *et al.* 2005), depriving arthropods of habitat while rates of mineralization and productivity of non-ant-prey organisms may increase. It is possible that ants exert top–down control in a trophic cascade, such that high topsoil P is actually the cause of ants indirectly increasing the decomposition of litter, facilitating P mineralization. Alternatively, the presence of common species in high P environments that grow slowly may be a consequence of greater competition, often cited as the 'hallmark of ant ecology' (Hölldobler & Wilson 1990). All organisms must allocate their energy among maintenance, growth, reproduction, and defense. Though P-rich sites offer more prey, the energy gained from prey might be spent on competitive interactions, and less common species may be those that grow more rapidly in high P environments.

Sets of soil nutrients significantly account for more variance in the size of ant nests than do either the biomass of standing fine litter or total fine litterfall inputs. In short, ant nest size is determined by the quality of resource more than the quantity of resource. Under the threshold element hypothesis, we considered that Ca may be limiting because of the high densities of oribatid mites, a preferred prey item of the common litter *Pheidole* (Wilson 2005). We found no support for Ca as a limiting element, as Ca was inversely related to nest densities of *Pheidole*, which consumes Ca-rich oribatid mites. Ca may not be a limiting nutrient for oribatid mites at La Selva. Alternatively, soil Ca may redirect the process of litter decomposition into a branch of the food web that does not include ants.

In summary, we have found that the heterogeneous distribution of nutrients across a tropical rain forest landscape explains much of the heretofore unaccounted variation in the density and size of ant nests within this forest. Mechanistic explanations will require integrative study of stoichiometry, physiology, litter processes, and food web structure. The natural history of tropical rain forest detrital systems (Moore *et al.* 2004), including the ants and their prey, remains in the descriptive phase. The associations we found highlight the limiting role of P in tropical forests while reinforcing the working hypothesis (Kaspari *et al.* 2008) that spatial differences in the relative abundance of several elements work in a non-linear fashion to direct the distribution of nutrients and energy in detrital food webs.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *The frequency of ant nests collected, sorted by the density of each species.*

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LITERATURE CITED

ANDERSEN, A. N. 1997. Using ants as bioindicators: Multiscale issues in ant community ecology. Cons. Ecol. 1: 8. http://www.consecol.org/vol1/iss1/art8/.

ANDERSEN, A. N., AND J. D. MAJER. 2004. Ants show the way Down Under: Invertebrates as bioindicators in land management. Front. Ecol. Environ. 2: 291–298.

ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois.

BEHMER, S. T., C. M. LLOYD, D. RAUBENHEIMER, J. STEWART-CLARK, J. KNIGHT, R. S. LEIGHTON, F. A. HARPER, AND J. A. C. SMITH. 2005. Metal hyper-accumulation in plants: mechanisms of defense against insect herbivores. Func. Ecol. 19: 55–66.

BERNSTEIN, R. A. 1975. Foraging strategies of ants in response to variable food density. Ecology 56: 213–219.

BYRNE, M. M. 1994. Ecology of twig-dwellings ants in a wet lowland tropical forest. Biotropica 26: 61–72.

CLARK, D. B., AND CLARK, D. A. 2000. Landscape-scale variation in forest structure and biomass in a tropical rain forest. For. Ecol. Man. 137: 185–198.

CLÉMENCET, J., AND C. DOUMS. 2007. Habitat-related microgeographic variation of worker size and colony size in the ant *Cataglyphis cursor*. Oecologia 152: 211–218.

CONNELL, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

CURRIE, D. J., G. G. MITTELBACH, H. V. CORNELL, R. FIELD, J. GUÉGAN, B. A. HAWKINS, D. M. KAUFMAN, J. T. KERR, T. OBERDORFF, E. O'BRIEN, AND J. R. G. TURNER. 2004. Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. Ecol. Lett. 7: 1121–1134.

DELHAIZE, E., AND P. R. RYAN. 1995. Aluminum toxicity and tolerance in plants. Plant Physiol. 107: 315–321.

DYTHAM, C. 2003. Choosing and using statistics, 2nd edition. Blackwell, Malden, Massachusetts.

ELSER, J. J., R. W. STERNER, E. GOROKHOVA, W. F. FAGAN, T. A. MARKOW, J. B. COTNER, J. F. HARRISON, S. E. HOBBIE, G. M. ODELL, AND L. W. WEIDER. 2000. Biological stoichiometry from genes to ecosystems. Ecol. Lett. 3: 540–550.

FRASER, R. H. 1998. Vertebrate species richness at the mesoscale: Relative roles of energy and heterogeneity. Global Ecol. Biogeogr. 7: 215–220.

FROST, P. C., AND J. J. ELSER. 2002. Growth responses of littoral mayflies to the phosphorus content of their food. Ecol. Lett. 5: 232–240.

GASTON, K. J. 2000. Global patterns in biodiversity. Nature 405: 220–227.

GOTELLI, N. J., AND A. M. ELLISON. 2002. Biogeography at a regional scale: Determinants of ant species density in New England bogs and forests. Ecology 83: 1604–1609.

HÖLLDOBLER, B., AND E. O. WILSON. 1990. The ants. Belknap Press of Harvard University Press, Cambridge, Massachusetts.

HUBBELL, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey.

HUTCHINGS, M. J., E. A. JOHN, AND D. K. WIJESINGHE. 2003. Toward understanding the consequences of soil heterogeneity for plant populations and communities. Ecology 84: 2322–2334.

JEYASINGH, P. D., AND L. J. WEIDER. 2005. Phosphorus availability mediates plasticity in life-history traits and predator-prey interactions in *Daphnia*. Ecol. Lett. 8: 1021–1028.

JONES, M. J., H. TUOMISTO, D. B. CLARK, AND P. OLIVAS. 2006. Effects of mesoscale environmental heterogeneity and dispersal limitation on floristic variation in rain forest ferns. J. Ecol. 94: 181–195.

KASPARI, M. 1996. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. Oikos 76: 43–454.

KASPARI, M., S. O'DONNELL, AND L. ALONSO. 2000. Three energy variables predict ant abundance at a geographic scale. Proc. Roy. Soc. Lond. B. 267: 485–490.

KASPARI, M., M. N. GARCIA, K. E. HARMS, M. SANTANA, S. J. WRIGHT, AND J. B. YAVITT. 2008. Multiple nutrients limit litterfall and decomposition in a tropical forest. Ecol. Lett. 11: 35–43.

MACARTHUR, R. H. 1969. Patterns of communities in the tropics. Biol. J. Linn. Soc. 1: 19–30.

MARAUN, M., J. ALPHEI, P. BESTE, M. BONKOWSKI, R. BURYN, S. MIGGE, M. ETER, M. SCHAEFER, AND S. SCHEU. 2001. Indirect effects of carbon and nutrient amendments on the soil meso- and microfauna of a beechwood. Biol. Fertil. Soils 34: 222–229.

MCGLYNN, T. P. 2006. Ants on the move: Resource limitation of a litter-nesting ant community in Costa Rica. Biotropica 38: 419–427.

MCGLYNN, T. P., R. R. DUNN, D. J. SALINAS, T. E. WOOD, D. LAWRENCE, AND D. A. CLARK. 2007. Phosphorus limits tropical rainforest litter fauna. Biotropica 39: 50–53.

MILTON, Y., AND M. KASPARI. 2007. Bottom-up and top-down regulation of decomposition in a tropical forest. Oecologia 153: 163–172.

MOE, S. J., R. S. STELZER, M. R. FORMAN, W.S DAUFRESNE, AND T. YOSHIDA. 2005. Recent advances in ecological stoichiometry: Insights for population and community ecology. Oikos 109: 29–39.

MOORE, J. C., E. L. BERLOW, D. C. COLEMAN, P. C. RUITER, Q. DONG, A. HASTINGS, N. C. JOHNSON, K. S. MCCANN, K. MELVILLE, P. J. MORIN, K. NADELHOFFER, A. D. ROSEMOND, D. M. POST, J. L. SABO, K. M. SCOW, M. J. VANNI, AND D. H. WALL. 2004. Detritus, trophic dynamics and biodiversity. Ecol. Lett. 7: 584–600.

NORTON, R. A., AND V. M. BEHAN-PELLETIER. 1991. Calcium carbonate and calcium oxalate as cuticular hardening agents in oribatid mites (Acari: Oribatida). Can. J. Zool. 69: 1504–1511.

PEETERS, C., AND F. ITO. 2001. Colony dispersal and the evolution of queen morphology in Hymenoptera. Ann. Rev. Entomol. 46: 601–630.

PORDER, S., P. M. VITOUSEK, O. A. CHADWICK, C. P. CHAMBERLAIN, AND G. E. HILLEY. 2007. Uplift, erosion and phosphorus limitation in terrestrial ecosystems. Ecosystems 10: 158–170.

POWERS, J. S., K. K. TRESEDER, AND M. T. LERDAU. 2005. Fine roots, arbuscular mycorrhizal hyphae and soil nutrients in four Neotropical rain forests: Patterns across large geographic distances. New Phytol. 165: 913–921.

REICH, P. B. 2005. Global biogeography of plant chemistry: Filling in the blanks. New Phytol. 168: 263–266.

REICHLE, D. E., M. H. SHANKS, AND D. A. CROSSLEY JR. 1969. Calcium, potassium and sodium content of forest floor arthropods. Ann. Ent. Soc. Am. 62: 57–62.

RITCHIE, M. E. 2000. Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. Ecology 81: 1601–1612.

SCHADE, J. D., M. KYLE, S. E. HOBBIE, W. F. FAGAN, AND J. J. ELSER. 2003. Stoichiometric tracking of soil nutrients by a desert insect herbivore. Ecol. Lett. 6: 96–101.

STERNER, R. W., AND J. J. ELSER. 2002. Ecological stoichiometry: The biology of elements from molecules to the biosphere. Princeton University Press, Princeton, New Jersey.

TABAK, L. M., AND K. E. GIBBS. 1991. Effects of aluminum, calcium and low pH on egg hatching and nymphal survival of *Cloeon triangulifer* McDunnough (Ephemeroptera: Baetidae). Hydrobiologia 218: 157–166.

TILMAN, D. 1994. Competition and biodiversity in spatially structured habitats. Ecology 75: 2–16.

VELDKAMP, E., A. BECKER, L. SCHWENDENMANN, D. A. CLARK, AND H. SCHULTE-BISPING. 2003. Substantial labile carbon stocks and microbial activity in deeply weathered soils below a tropical wet forest. Global Change Biol. 9: 1171–1184.

VITOUSEK, P. M., AND R. L. SANFORD. 1986. Nutrient cycling in moist tropical forest. Ann. Rev. Ecol. Syst. 17: 137–167.

WASSEN, M. J., H. O. VENTERINK, E. D. LAPSHINA, AND F. TANNEBERGER. 2005. Endangered plants persist under phosphorus limitation. Nature 437: 547–550.

WHITTAKER, R. J. 2000. Scale, succession and complexity in island biogeography: Are we asking the right questions? Global Ecol. Biogeography 9: 75–85.

WILSON, E. O. 1971. The insect societies. Belknap, Cambridge, Massachusetts.

WILSON, E. O. 2005. Oribatid mite predation by small ants of the genus *Pheidole*. Ins. Soc. 52: 263–265.

WOOD, T. E., D. LAWRENCE, AND D. A. CLARK. 2005. Variation in leaf litter nutrients of a Costa Rican rain forest is related to precipitation. Biogeochemistry 73: 417–437.

WOOD, T. E., D. LAWRENCE, AND D. A. CLARK. 2006. Determinants of leaf litter nutrient cycling in a tropical rain forest: Fertility versus topography. Ecosystems 9: 700–710.