Biogeochemistry and the structure of tropical brown food webs

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Abstract. Litter invertebrates are notoriously patchy at small scales. Here we show that the abundance of 10 litter taxa also varies 100-fold at landscape and regional scales across 26 forest stands in Peru and Panama. We contrast three hypotheses that link gradients of abundance to ecosystem biogeochemistry. Of 14 factors considered (12 chemical elements, plus fiber and litter depth), four best predicted the abundance of litter invertebrates. In the Secondary Productivity Hypothesis, phosphorus limits abundance via the conversion of detritus to microbial biomass. Two of four microbivore taxa, collembola and isopods, increased with the percentage of P (%P) of decomposing litter. However, percentage of S (correlated with %P) best predicted the abundance of collembola, oribatids, and diplopods (r^2 = 0.38, 0.33, 0.21, respectively). In the Structural Elements Hypotheses, N and Ca limit the abundance of silk-spinning and calcareous taxa, respectively. Mesostigmatids, pseudoscorpions, and spiders, all known to make silk, each increased with percentage of N of litter (r^2 = 0.22, 0.31, 0.26, respectively). Calcareous isopods, but not diplopods, increased with percentage of Ca of litter (r^2 = 0.59). In the Ecosystem Size Hypothesis, top predators are limited by available space. The abundance of the three remaining predators, chilopods, staphylinids, and ants, increased with litter depth (r^2 = 0.31, 0.74, 0.69, respectively), and food webs from forests with deeper litter supported a higher ratio of predators to microbivores. These results suggest that biogeochemical gradients can provide a mechanism, through stoichiometry and trophic theory, shaping the geography of community structure.

Key words: calcium; decomposition; ecosystem size; invertebrates; litter; nitrogen; phosphorus; stoichiometry; trophic structure; tropical forests.

INTRODUCTION

A primary goal of ecology is to understand how taxon abundance varies from place to place. Since organisms are built from ~25 chemical elements (Frausto da Silva and Williams 2001), gradients of biogeochemistry provide a potential mechanism generating gradients in consumer abundance (Hessen 1992, Orians and Milewski 2007). Herbivores and decomposers appear to be particular candidates for stoichiometric control: both convert low-quality plant tissue into high-quality heterotroph tissue (Sterner and Elser 2002). But any taxon's abundance may track an element in time and space, if that taxon is built from large quantities of a relatively rare element.

Standardized abundance data for terrestrial consumers are relatively rare at landscape and regional scales. Tropical brown food webs (BFWs)—detritus, decomposers, and their consumers—are model systems toward building such data sets. Brown food webs exist as a thin layer of easily sampled detritus resting on mineral soil

(Swift et al. 1979, Moore et al. 2004). Gradients in the activity and abundance of these organisms have obvious implications for ecosystem function. Brown food webs convert >90% of leaf production, falling uneaten to the tropical forest floor (Coley and Barone 1996), into tissue, soil organic matter, mineralized nutrients, and CO_2 (Moore et al. 2004). If multiple nutrients limit the action of microbes and their consumers, then the rates of these ecosystem fluxes may in turn map onto gradients of biogeochemistry.

Here we explore the structure of BFWs across 26 Neotropical forest stands, focusing on 10 widespread taxa readily sampled with quadrats. They can be grouped as microbivores and predators. Four taxa consume microbes in two different ways. Collembola and oribatid mites tend to graze bacterial and fungal turfs (Moore et al. 1988). Isopods and diplopods, in contrast, consume microbe-covered detritus. They digest some of the litter with the help of endosymbionts, but also gain nutrients from the free-living microbes they ingest (Swift et al. 1979, Zimmer 2002). We hence group all four taxa as microbivores, but return to the implications of these two modes of foraging in the *Discussion*. In tropical forests, microbivores tend to have a net positive effect on decomposition rates (Heneghan

et al. 1999, Milton and Kaspari 2007) by removing inactive microbes and through the digestion and fragmentation of the detritus itself (Hanlon 1981, Moore et al. 1988, Teuben 1991).

Tropical BFWs also include a diversity of predators. The six predator taxa (mesostigmatid mites, pseudoscorpions, spiders, chilopods, staphylinid beetles, and ants) consume microbivores (Swift et al. 1979, Scheu and Setala 2002). Both trophic levels are abstractions, masking individual and population variability, but are used here as simplified working hypotheses (Scheu and Falca 2000, Andre et al. 2002) to test broader hypotheses on the control of abundance at landscape and regional scales.

The varied roles of BFWs in ecosystems and their ease of study suggest that a model for the biogeography of BFWs is both overdue and achievable (Swift et al. 1979, Moore et al. 2004). We evaluate three models that may help serve this goal. They are not mutually exclusive, but instead emphasize how the conversion of food into microbial biomass, the availability of elements required to build taxon-specific structures, and the quantity of litter habitat shape the abundance of litter invertebrates.

Secondary productivity: the conversion of detritus to microbivore food

The microbivores of the BFW feed on microbial biomass. A hierarchy of factors limit the rate that carbon-rich detritus is converted to microbial biomass (i.e., decomposition; Moore et al. 2004). Globally, primary productivity and decomposition rate increase with the co-availability of water and solar energy (Rosenzweig 1968, Allen et al. 2005). Tropical forests, however, occupy the high end of earth's water and solar energy gradients (Meetemeyer 1978). In such forests, phosphorus availability experimentally limits litter decomposition (Hobbie and Vitousek 2000, Kaspari et al. 2008). This is likely so for two reasons. First, old tropical soils are leached of phosphorus (Walker and Syers 1976). Second, fast-growing microbes have a high demand for P-rich ribosomes (Elser et al. 1996, Gillooly et al. 2005). Combined, this suggests that the secondary production of microbial biomass should increase along gradients of available P. In fact, across the 26 forest stands studied here, ecosystem P is negatively correlated with litter depth ($r^2 = 0.76$; Kaspari and Yanoviak 2008).

The Secondary Productivity Hypothesis assumes that the percentage of phosphorus (%P) of decomposing litter at the time of sampling is a proxy for the production of microbial biomass from detritus. We test the simple prediction that the abundance of microbivores increases along gradients of litter P.

Ecosystem size: Does deeper litter add predators?

Consider for a moment a key difference between terrestrial green and brown food webs. In green food webs (GFWs), increases in primary productivity at the base of the web (i.e., moving from desert pavement to grasslands to forests) represents a joint increase in the supply of food and habitat space (Whittaker 1966). This is not the case for the secondary production at the base of BFWs, where microbes feed microbivores by consuming their habitat (Moore et al. 2004). Thus where net primary productivity is roughly equal, increases in microbial productivity should decrease litter habitat as detritus is converted to microbial biomass and CO_2 (Kaspari and Yanoviak 2008).

There may be considerable consequences for BFWs when deeper litter results from lower microbial productivity. The litter habitat consists of overlapping surfaces that grow smaller and more granular with depth (Swift et al. 1979, Moore et al. 2004). As litter accumulates so do the surfaces available for litter arthropods to walk upon, graze from, and hide between. The Ecosystem Size Hypothesis (Post et al. 2000) makes two assumptions. First, larger areas support more species. Second, more species allow for more trophic levels (Cohen and Newman 1992). The hypothesis predicts that larger predators are disproportionately limited by the amount of habitat relative to their prey. For example, carnivore home range sizes tend to be larger and scale more steeply than those of herbivores (Jetz et al. 2004).

As noted above, the litter habitat of the BFW is best measured as a volume of overlapping planes. Extending the Ecosystem Size Hypothesis to the litter, then, predicts that (1) predator taxa should accumulate with litter volume, and, similarly (2) forests with the shallowest litter should support primarily small microbivores.

Structural elements: you eat what you are

Sometimes it's not food production, but the concentration of nutrients or toxins in that food that limits abundance (Rosenthal and Janzen 1979, Simpson et al. 2004). The stoichiometry and dietary requirements of microbes, microbivores, and predators can vary given the chemistry of their functional traits (Sterner and Elser 2002, Karimi and Folt 2006). In the Structural Elements Hypothesis, the building blocks of traits such as the P-rich bones of vertebrates, the calcareous skeletons of many invertebrates, and the silicaceous tests of diatoms are rare enough in the environment to limit growth. It assumes that populations in environments with low quantities of these structural elements will grow more slowly and, all else equal, maintain smaller population sizes (Hessen 1992, Sterner and Elser 2002). The Structural Elements Hypothesis is thus likely to be important when a high demand for a structural element by a taxon is combined with environmental gradients in its availability.

Two suites of taxa in the BFW are candidates for the Structural Elements Hypothesis. The calcareous exoskeletons of the first group, isopods and diplopods, may comprise ≥10% whole-body Ca by mass (Gist and Crossley 1975, Ziegler et al. 2007). Litter calcium

availability can vary widely across the landscape due to differing inputs in leaf litter (Reich et al. 2005) and differing concentrations across and within fungal species (Wainwright 1992).

A second group—spiders, pseudoscorpions, and some mesostigmatid mites—are three arachnid predators that produce N-rich silk (Xu and Lewis 1990, Craig 2003). Silken webs are energetically costly and must be repeatedly constructed and repaired (Ford 1977, Tanaka 1989). Furthermore, silk webs may be 50% richer in N than the bodies that produce them; Fagan and colleagues (2002) report whole-body N for spiders at ~11.5% while the amino acid content of silk reported by Xu and Lewis (1990) yields an estimate of 17.4% N. Likewise, the availability of N varies within ecosystems across prey types (Fagan et al. 2002) and across ecosystems with geography and age (Walker and Syers 1976).

Applying the Structural Elements Hypothesis to the BFW, we thus predict that isopods and diplopods should increase along gradients of ecosystem Ca and that spiders, pseudoscorpions, and mesostigmatids will increase along gradients of N.

Here we test the general hypothesis that the abundance and trophic structure of tropical lowland BFWs parallel gradients of biogeochemistry given the latter's effects on (1) P-based microbial productivity, (2) litter depth that disproportionately limits predators, and (3) Ca- and N-based structural traits. We use stepwise regression to screen 12 elements often linked to consumer performance across 10 forest stands in Panama and 16 in Peru. We show that the depth of litter and its N, S, and Ca content account for between 20% and 74% of the variation in the abundance of these 10 common taxa.

Methods

Litter depth, chemistry, and litter invertebrates were sampled from 28 lowland forest stands in Panama and Peru with similar rainfall (2400–2700 mm/yr). Ten stands were sampled from the forests of Barro Colorado Nature Monument (BCNM) in the Republic of Panama (9°06′ N, 79°50′ W). The species composition and stature of these forests are characteristic of an old (>300 yr) high-canopy seasonal forest with ~2400 mm annual rainfall. A previous survey of the island (Knight 1975) was used to identify 10 stands on clay oxisols with a range of soil fertility. Forest stands were sampled in June and July 2004 near the beginning of the wet season. The minimum distance between stands was ~0.5 km.

Eighteen stands of lowland forest were sampled around the city of Iquitos in Loreto Province, northeastern Peru (4°00′ S, 73°30′ W). We sampled two types of high-canopy forest: clay oxisols and ultisols (Vitousek and Sanford 1986) and sandy soils (Anderson 1981). These forests have grossly similar vegetation structure but differing tree species (Fine et al. 2004). The region is roughly aseasonal, receiving 2400–2800 mm annual

rainfall; our sampling from February to May 2004 included the wettest months. All stands were located between highway kilometer markers 10 and 60 (km 0 is in Iquitos) and within 3 km due east or due west of the road. The minimum distance between replicate forests within a soil type was ~150 m.

At each of the 28 forest stands, we collected leaf litter from five sampling quadrats spaced 5 m apart on a 25-m transect. The starting point for each transect was selected haphazardly, and all sampling points were >50 m from a forest edge. Litter depth was measured in each corner of a PVC frame by inserting a surveyor's flag marked in 1-cm increments down to mineral soil. Leaf litter (excluding woody material >4 cm in diameter) inside the frame was collected down to mineral soil by hand. A uniform fine litter siftate was extracted through the 1-cm mesh of a hand-held litter sifter for 30 s and stored in cloth bags for extraction ~2–4 h later. Since litter was deeper in Peru, and to standardize siftate quantity, Peru quadrats were smaller (0.125 m^2 vs. 0.25 m^2 in Panama). Tullgren funnels (40-W incandescent bulb, 48–72 h) were used to separate arthropods from the siftate into 95% ethanol (siftate samples >1000 mL volume were divided between two funnels to improve extraction efficiency). Tullgren funnels are the most common standardized method for extracting soil arthropods and extract taxa with different degrees of effectiveness (Andre et al. 2002). Our goal was to compare gradients of relative abundance within and between taxa.

After extraction, the remaining mix of litter + microbes was analyzed for elements potentially limiting consumers (Table 1). Two 10-g subsamples were analyzed at the Oklahoma State Soil, Water, and Forage Analytical Laboratory (Stillwater, Oklahoma, USA), using a combination Lachat flow injection autoanalyzer (Lachat, Loveland, Colorado, USA), Spectro CirOs ICP [Inductively Coupled Plasma] spectrometer (Spectro, Kleve, Germany), and an Ankom fiber analyzer (Ankom, Macedon, New York, USA). The mean value of the two samples was used to characterize each forest stand. The litter from one pair of Peru sites was lost before this analysis could be performed, leaving us with 10 Panama and 16 Peru forest stands with litter chemistry.

Statistics

We explored the effects of geography and soil type comparing Panama with Peru and clay and sandy soils within Peru. We used taxa that were found in at least 26 of the 28 forest stands and could roughly be assigned to one of two trophic groups (Ponsard and Arditi 2000, Scheu and Falca 2000). Microbivores/shredders (henceforth microbivores) included collembola, oribatid mites, diplopods, and isopods (other shredders, such as earthworms [Bohlen et al. 2004] and termites [Wood 1976], were not common in our plots). Predators included mesostigmatid mites, pseudoscorpions, spiders,

TABLE 1. Litter depth and chemistry (leaf litter + microbes) of sites compared regionally between Panama and Peru and between clay and sand soils in Peru.

| Litter variable | Regional comparison | | | Soil comparison | | | PC 1 (61%) | PC 2 (17%) |
	Panama ($n = 10$)	Peru ($n = 16$)	χ^2	Clay ($n = 8$)	Sand ($n = 8$)	χ^2		
Depth (cm)	2.0	8.5	18.6**	5.7	12.8	12.2**	−0.3	0.1
% NDF	64	69	4.9*	65	72	7.4**	...	...
% C	39	42	0.71	36.3	46.9	5.8*	...	...
% N	1.7	1.9	2.8	1.8	2.0	0.2	−0.1	0.6
% P	0.09	0.05	15.4**	0.06	0.05	1.9	0.3	0.2
% K	0.11	0.08	5.6*	0.10	0.06	8.8**	0.3	0.1
% Ca	2.0	0.8	8.7**	1.3	0.3	4.4*	0.3	0.2
% Mg	0.3	0.1	10**	0.18	0.04	6.4*	0.4	0.1
% Na	0.008	0.005	13.6**	0.0054	0.0036	5.1*	0.3	0.3
% S	0.19	0.15	7.8*	0.16	0.14	3.0	0.3	0.1
Fe (ppm)	33 000	5900	13.6**	11 000	1100	11.3**	0.3	−0.3
Zn (ppm)	77	79	0.1	86.4	70.9	1.1	0.1	−0.4
Cu (ppm)	51.7	30.8	5.9*	30.3	31.2	0.5	0.2	−0.5
Mn (ppm)	1000	378	10.7**	609	148	5.3*	0.3	0

Notes: For comparisons, χ^2 is the two-tailed Kruskal-Wallis statistic. The last two columns report the loadings on the first two principal components (PC) for $\log_{10}$-transformed values of all but carbon and neutral detergent fiber (NDF), rounded to 0.1. The percentage of variation described is given in parentheses in the column heads.

* $P < 0.05$; ** $P < 0.01$.

chilopods, staphylinid beetles, and ants. Following Scheu and Falca (2000) we treat these trophic assignments as working hypotheses that mask some trophic diversity within these tropical taxa.

We compared abundances of adults and juveniles (in numbers per square meter) between Panama and Peru and between Peru soil types using Kruskal-Wallis tests. We examined the correlation structure of 10 variables (log percentages of all elements but carbon, plus litter depth) using principal components analysis (PCA). We tested hypotheses linking abundance to biogeochemistry by regressing $\log_{10}$(abundance) against $\log_{10}$(elemental chemistry) (by percentage of dry mass). This yielded power functions, which assume multiplicative relationships between resource supply and abundance. We used stepwise regression to identify the best one-variable model predicting abundance. We repeated the analysis for Panama ($n = 10$) and Peru ($n = 16$) forests separately to quantify regional differences (ANCOVA was not used, as the assumption that independent variables are homogeneously distributed across the two regions often did not hold).

To test the hypothesis that space-limited predators increasingly dominate BFWs, we regressed the ratio of microbivore abundance to predator abundance against the array of variables above. Finally, we regressed the abundance of all 10 taxa against %P (Secondary Productivity Hypothesis), calcareous taxa against percentage of Ca (%Ca) and silk spinning taxa against percentage of N (%N) (Structural Elements Hypothesis) and all predator taxa against litter depth (Ecosystem Size Hypothesis) to evaluate the performance of these specific models.

RESULTS

The assumption of biogeographic gradients in litter depth and nutrient availability was supported across the 16 sites (Table 1). Average litter depth varied 16-fold (1.37–22.4 cm) and was fourfold deeper on average in Peru, where it was twice as deep on sandy vs. clay soils. Decomposing litter from Panama was generally richer in minerals (Table 1), with about five times as much Fe, three times as much Mn and Mg, twice as much P, Ca, and Na, 40% more K, and 25% more S. In Peru, decomposing litter on clay soils had 25% less C, but more K, Ca, Mg, Na, Fe, and Mn than on sandy soils. Only Zn and N concentrations failed to vary systematically with region or soil type. Principal components analysis revealed a general gradient of increasing nutrients in decomposing litter for all elements but N, accounting for 61% of the variation in the data set (Table 1). The second axis described an inverse relationship between N and three metals, particularly Zn and Cu, accounting for an additional 17% of the variation.

As the PCA suggests, some potential driver variables were correlated. Specifically, of the variables posited (or discovered) to be potential drivers of abundance, P correlated positively with Ca (Pearsons correlation, $r_p = 0.86$) and S ($r_p = 0.77$), negatively with litter depth ($r_p = -0.80$, all three, $P < 0.0001$), and was uncorrelated with N ($r_p = -0.06$, $P = 0.76$). Calcium correlated positively with S ($r_p = 0.77$), negatively with litter depth ($r_p = -0.79$, both, $P < 0.0001$), and was uncorrelated with N ($r_p = 0.04$, $P = 0.84$). Nitrogen was uncorrelated with S ($r_p = 0.24$, $P = 0.23$) and positively correlated with litter depth ($r_p = 0.40$, $P = 0.04$). Sulfur was negatively correlated with litter depth ($r_p = -0.62$, $P = 0.0007$). Thus between 23% and 99% of variation in one of these litter variables was unaccounted for by the variation in another.

Like biogeochemistry, invertebrate abundance varied widely across the forest stands (Fig. 1, Table 2). Microbivore and predator taxa typically varied >100-
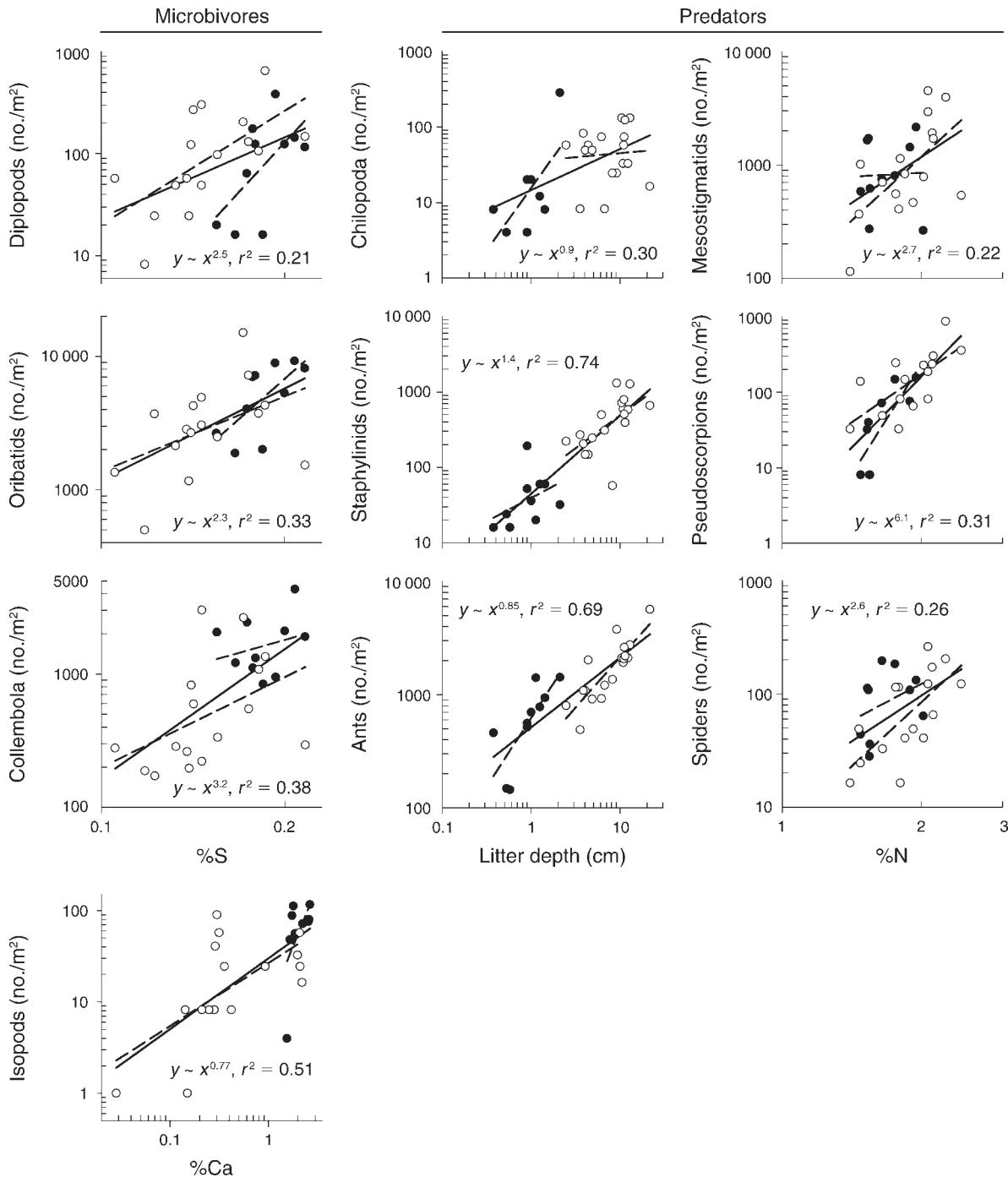
FIG. 1. The best predictors of abundance of 10 litter invertebrates from 26 tropical forest stands in Panama and Peru. Four litter variables from a list of 14 (log$_{10}$[litter depth], neutral detergent fiber, and percentages of C, N, P, Ca, K, Mg, Na, S, Fe, Zn, Cu, and Mn in litter residuum) were chosen by multiple regression. The solid lines represent regressions across all sites; the dashed lines represent regressions for Peru (open circles) and Panama (solid circles).

fold. The smallest arthropods (collembola, oribatids, and mesostigmatids) often numbered in the thousands per square meter, as did the density of worker ants. Two microbivore taxa, the collembola and isopods, were two

to three times more abundant in Panama. Four predator taxa (pseudoscorpions, chilopods, staphylinids, and ants) were more common in Peru; staphylinids and ants were more common on sandy soils in Peru.

TABLE 2. Abundance (number/m^2) of 10 common litter taxa compared regionally between Panama and Peru and between clay and sandy soils in Peru.

	Regional comparison			Soil comparison		
Taxon	Panama ($n = 10$)	Peru ($n = 16$)	χ^2	Clay ($n = 8$)	Sand ($n = 8$)	χ^2
Microbivores						
Collembola	1800	859	7.0*	680	1000	0.1
Oribatids	5600	4500	1.2	3900	5000	0.2
Isopods	70	27	7.8**	26	27	0.1
Diplopods	118	169	0.3	192	145	0.0
Predators						
Mesostigmatids	1000	1400	0.2	1500	1300	0.2
Pseudoscorpions	54	195	6.3*	142	248	0.5
Spiders	101	96	0.1	94	98	0.3
Chilopods	36	57	9.5**	45	69	0.8
Staphylinids	50	495	16.6**	371	619	4.0*
Ants	707	2000	10**	1400	2500	7.3**

Note: For comparisons, χ^2 is the two-tailed Kruskal-Wallis statistic.
* $P < 0.05$; ** $P < 0.01$.

Microbivores

Litter S best predicted the abundance of three of the four microbivores ($r^2 = 0.38$ for collembola, 0.33 for oribatid mites, and 0.21 for diplopods; Fig. 1). The exponents in each case suggest an accelerating increase in abundance with increasing %S. Calcium best predicted the abundance of isopods, the fourth microbivore taxon. Isopods showed a nearly linear ($b = 1.1$) increase with the %Ca of decomposing litter ($r^2 = 0.51$; Table 3).

When these results were tested for each region, the exponents roughly mirror the global pattern, although the P values reflect the smaller sample sizes (Fig. 1, Table 3). The exponents of the %S–abundance relationships are similar, but P values often exceed 0.05 for collembola (Panama, $P = 0.46$; Peru, $P = 0.08$), oribatids (Panama, $P = 0.03$; Peru, $P = 0.09$), and diplopods (Panama, $P = 0.06$; Peru, $P = 0.0095$). Similarly, the ability of %Ca to predict isopod abundance is marginally significant in Panama ($P = 0.09$) compared to Peru ($P = 0.0082$).

Two microbivores, collembola and isopoda, increased along gradients of %P, consistent with the Secondary Productivity Hypothesis (Table 3).

One of two calcareous taxa, the isopods, but not the diplopods, increased along gradients of %Ca, consistent with the Structural Elements Hypothesis.

Predators

Nitrogen best predicted the abundance of the three silk-spinning predators (pseudoscorpions, spiders, and mesostigmatid mites; $r^2 = 0.31$, 0.26, and 0.22, respectively), consistent with the Structural Elements Hypothesis. In all three cases, abundance increased exponentially with %N (all $b > 2.6$). However, when samples were split, gradients of %N predicted the abundance of three arachnid taxa in Panama, but not in Peru (mesostigmatids, Peru, $P = 0.91$, Panama, $P = 0.01$; pseudoscorpions, Peru, $P = 0.87$, Panama, $P = 0.002$; spiders, Peru, $P = 0.30$, Panama, $P = 0.003$).

Litter depth best predicted the abundance of chilopods, staphylinids, and ants consistent with the Ecosystem Size Hypothesis. The abundance of staphylinids and ants, in particular, increased relatively uniformly ($b = 1.4$ and 0.85; Fig. 1, Table 3) with litter depth accounting for 74% and 69% of total variation. Litter was thinner in Panama than Peru, and failed to predict the abundance of chilopods in either region (Panama, $P = 0.07$; Peru, $P = 0.78$). Staphylinids increased significantly with litter depth only in Peru (Panama, $P = 0.32$; Peru, $P = 0.0064$). The abundance of ants increased with litter depth at both sites (Peru, $P = 0.007$; Panama, $P = 0.0001$).

No predator taxa increased with %P; two taxa, ants and staphylinids, decreased along this gradient (Table 3).

Four predator taxa (chilopods, staphylinids, ants, and pseudoscorpions) increased with litter depth, consistent with the Ecosystem Size Hypothesis (Table 3).

Trophic structure

The ratio of microbivore to predator abundance ranged from 0.19 (i.e., one microbivore for five predator individuals) in a Peru sandy forest to 6.4 (six microbivores to one predator) in a Panama forest stand (Fig. 2). The ratio was best predicted by litter depth with which it declined rather uniformly ($y = 7.0x - 0.88$, $r^2 = 0.69$, $F_{1,25} = 53.8$, $P < 0.0001$).

DISCUSSION

In the lowland tropics, brown food webs occupy a thin layer of decomposing leaves and debris typically no more than a few centimeters deep. Here we show 100-fold variation in the abundance of BFW taxa at the landscape and regional scale. We then build a plausible case that some of this variation can be linked to a handful of essential elements that are either structural components (N and Ca) or underlie productivity and habitat space (P). Combined with local experimental tests of bottom-up limitation (Scheu and Schaefer 1998,

TABLE 3. Regression (as a power function, $y = ax^b$) of abundance (number/m^2) against percentage of elemental composition of decomposing litter for 10 litter taxa.

y	Multiple regression				By region		Models			
	x	r^2	a	b_{total}	b_{Panama}	b_{Peru}	$x = P$	$x = Ca$	$x = N$	$x = LD$
Microbivores										
Collembola	S	0.38	270 000	3.2**	1.3	2.2	1.6**			
Oribatids	S	0.33	220 000	2.3**	4.0*	1.9	0.7			
Diplopods	S	0.21	8700	2.5**	6.3	3.6**	0.5	0.2		
Isopods	Ca	0.51	31	0.8**	2.5	0.7**	2.4**	0.8**		
Predators										
Mesostigmatids	N	0.22	182	2.7*	0.24	3.7*	0.2		2.7*	0.1
Pseudoscorpions	N	0.31	1.65	6.1**	0.77	6.6**	−1		6.1**	1**
Spiders	N	0.26	15.8	2.6**	2.1	3.7**	0.8		2.6**	0.1
Chilopods	LD	0.31	5.3	1.0**	4	0.11	−1.1			1.0**
Staphylinids	LD	0.74	17	1.4**	1.1	1.0**	−3.1**			1.4**
Ants	LD	0.69	316	0.9**	2.6**	1.0**	−1.4**			0.9**
Micro : Predator	LD	0.63	6.9	−0.8**	−0.67	−0.62				−0.8**

Note: The best predictors of abundance, of 14 litter variables, are followed by exponents for data which are divided by region (Panama, $n = 10$; Peru, $n = 16$). The final four columns give exponents from tests of the Secondary Productivity Hypothesis (P), the Structural Elements Hypothesis (Ca and N), and the Trophic Space Hypothesis (litter depth, LD). "Micro : Predator" is the ratio of microbivores to predators in a sample.

* $P < 0.05$; ** $P < 0.01$.

Milton and Kaspari 2007), these results point to new opportunities in generating a mechanistic spatial ecology of tropical brown food webs.

Structural elements and secondary productivity: toward a nutritional ecology of BFWs

The correlations of animal abundance to gradients of Ca and N are the first we know of to suggest that the stoichiometry of costly functional traits can be profitably scaled up to study the geography of abundance (Karimi and Folt 2006, Orians and Milewski 2007). Herbivores have long been thought to be N-limited (White 1978) and N fertilization has increased microbivores and detritivores in a temperate zone grassland (Haddad et al. 2000, Cole et al. 2005). Predators, in contrast, tend to consume N-rich flesh and thus would appear less likely to be nitrogen limited. However, here we show that three of six predator taxa (all arachnids reported to generate N-rich silk) tracked gradients of N in decomposing litter. This result is given further credibility as concentrations of litter N were not obviously confounded with those of Ca or P. Likewise, isopods and diplopods invest 10+% of body mass in a calcareous exoskeleton (Gist and Crossley 1975, Ziegler et al. 2007). Half the variation in isopod abundance, but not that of diplopods, could be accounted for by the 100-fold gradient in litter Ca. The failure of diplopods to track Ca is a puzzle. Below we suggest diplopod abundance at a geographic scale may be more strongly driven by predation risk.

The Secondary Productivity Hypothesis assumes that elements limiting the production of microbial biomass will similarly predict the abundance of microbivores. Phosphorus is often linked to the metabolism of plants and microbes in tropical forests given that weathering depletes this rock-born element (Walker and Syers 1976, McGroddy et al. 2004, Kaspari et al. 2008). The Secondary Productivity Hypothesis predicted the positive association between %P and the abundance of collembola ($P < 0.006$) and isopods ($P < 0.002$) but not oribatids and diplopods ($P > 0.08$).

Instead, the abundance of three of four common microbivore taxa was best predicted by litter sulfur. Sulfur could enhance the abundance of microbivores as a limiting nutrient (Frausto da Silva and Williams 2001); it may also be an indirect assay of litter quality if plants (Bloem et al. 2005) or microbes (Wicklow 1981) invest more S-based defenses in nutrient-rich leaves. However, the three elements implicated by regression to be correlated with microbivore abundance, S, Ca, and P, are themselves correlated across the 26 forest stands studied (Table 1). Thus a third working hypothesis, that
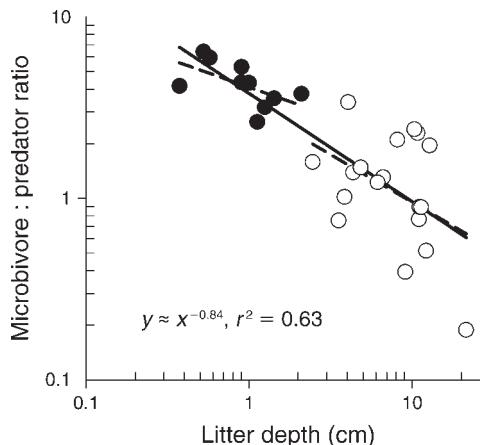

FIG. 2. The ratio of microbivore to predator abundance in a 1-m^2 plot is best predicted by litter depth from a list of 14 variables (see Fig. 1). The solid line represents the regression across all sites; the dashed lines represent regressions for Peru (open circles) and Panama (solid circles).

also has the benefit of parsimony, is that phosphorus drives microbial productivity (Kaspari and Yanoviak 2008, Kaspari et al. 2008), which in turn enhances the abundance of the microbivores. The role of P is given some support by the increases in S and Ca concentrations in litterfall when plots were fertilized with P in a Panama forest (Kaspari et al. 2008). However, elements play multiple, synergistic roles in metabolism (Frausto da Silva and Williams 2001, Simpson et al. 2004); the regressions reported here are thus only a first, significant step toward predicting abundance at landscape and regional extents. Studies linking diet, preference, and performance (Simpson and Raubenheimer 1996, 2001, Frost et al. 2006) and factorial fertilization experiments (Kaspari et al. 2008) will complement the geographical comparisons presented here (Diamond 1986). For example, preliminary data suggest that collembola and oribatid biomass increases on Panama plots fertilized with phosphorus (M. Kaspari, *unpublished data*). The top-down effects of predators may also play a role in generating patterns of microbivore abundance, as we discuss next.

Ecosystem size: more litter habitat shifts the trophic balance

Litter depth in these lowland forests varied from the shallow litter of the most phosphorus-rich stands on BCNM to the deep mulder of the Peruvian white sands. Consistent with the Ecosystem Size Hypothesis, chilopods, staphylinids, and ants increased with litter depth. In contrast to microbivore responses, staphylinids and ants decreased with litter phosphorus (Table 3). The declining ratio of microbivore to predator abundance across forest stands further supports the hypothesis that deep litter disproportionately favors predators. It also suggests that the strength of top-down interactions, as mediated by available litter depth, may increase when decomposition slows (Lawrence and Wise 2000, Scheu and Setala 2002). Top-down interactions may be common in the tropical litter: pulses of P and N can enhance the abundance of predacious ants, but not their microbivore prey, presumably because the ants absorbed increases in microbivore production (Milton and Kaspari 2007); tropical mesocosms devoid of ants and spiders experience population explosions of collembola (M. Kaspari, *unpublished data*).

One interesting difference between green and brown food webs is the status of a related hypothesis, the Productive Space Hypothesis (Schoener 1989, Post 2007), in which both food supply and living space increase together, favoring the accumulation of top predators. To be applicable to BFWs, the Productive Space Hypothesis would require that both litter depth and microbial production increase together. However, as litter must be degraded to generate microbial biomass, such a state could not long endure.

Ultimately, experimental manipulations of litter depth (Osler et al. 2006, Sayer et al. 2006) are easy to do at large scales. Such experiments offer the potential for further separating the mechanisms of the Ecosystem Size Hypothesis from other effects of increasing litter depth, such as changes in pH, oxygen, and moisture (Sayer 2005).

Caveats

These data attack the question of ecological abundance at large spatial scales and high taxon aggregation. However, ecological patterns are sensitive to the degree of taxonomic resolution (Kaspari 2001). For example, N fertilizers increased the abundance of microbes at the base of a temperate BFW (Scheu and Schaefer 1998); furthermore, while microbivores as a group did not change with fertilization, the abundance of some common species of isopods and diplopods responded to added N, P, and/or glucose. This suggests further insights will be gained by tunneling into BFWs both taxonomically and functionally (Ponsard and Arditi 2000). Doubtless our forests stands, with some of the highest recorded diversity of litter arthropods (Kaspari et al. 2003), will reveal a more complex reality when we do so. We are encouraged, however, to find patterns consistent with theory even at high levels of aggregation.

Likewise, many of the gradients of abundance discussed here weaken (though none change sign) when divided regionally. Many times this may be ascribed to a commensurate decrease in the range of values along the x-axis (e.g., %Ca, %S, and litter depth). However, we cannot rule out the possibilities of either regional or scale-specific (Kaspari et al. 2003) regulation of abundance.

Conclusions and speculations

While four of six predator taxa were more common in the deep litter of Amazon forests, two of the four microbivore taxa, collembola and isopods, were more abundant in the phosphorus-rich but shallow-litter forests of Panama (Table 2). A cursory literature review and our own experience indicate that chemical defenses, alkaloids, p-benzoquinones, phenols, cyanogens, and quinazolinones, are more common among the two microbivore taxa that do not show this pattern: the oribatids and diplopods (Eisner et al. 1978, Dettner et al. 1996, Saporito et al. 2007).

This suggests a working hypothesis that nutrients shape the structure of BFWs in multiple, related ways. First, P-rich forests promote high decomposition rates (and thus high food availability). In the process, through direct decomposition and by encouraging the actions of shredders, microbes eliminate the deep litter haven of predators such as ants and staphylinid beetles, reducing microbivore mortality. Such a pattern was found across temperate agroecosystems, where high input fields with little litter also had a dearth of BFW predators (Mulder et al. 2005).

Similarly, nutrient-poor soils also produce a cascade of effects. Our impoverished forest stands in Amazonia select for tough, phenolic-rich leaves defended against

herbivory (Coley et al. 1985, Fine et al. 2004). Leaf litter from sandy soils in Peru had 13% more neutral detergent fiber than clay soils. As recalcitrant litter accumulates, decomposition rates may be further retarded as deep litter provides habitat for predators, selecting against microbivores with high metabolisms and, in turn, favoring microbivores with chemical defenses.

The summed effect may be that the competitive balance of microbivore life histories, like those of plants (Coley et al. 1985, Fine et al. 2004), varies along biogeochemical gradients: rich environments favor fast growers with few defenses (collembola and isopods), poor environments favor slow growers heavily invested in defenses (diplopods and oribatids). Furthermore, the causal relationship between litter depth and predator abundance may be self-reinforcing. Brown food web predators can suppress microbivore populations (Lawrence and Wise 2000, Milton and Kaspari 2007). Microbivores in turn can enhance decomposition (Milton and Kaspari 2007). This suggests that the association between deep litter and predator abundance may be at least partially engineered by the predators themselves.

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