Trees as templates for trophic structure of tropical litter arthropod fauna

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ABSTRACT

Litter arthropod abundance in tropical forests is patchily distributed in space and time. This patchiness can be described by three general hypotheses relating plant-based effects to litter arthropod distribution. The tree hypothesis (H1) posits that environments maintained underneath tree canopies are different from those between canopies in ways that shape arthropod abundance. The species hypothesis (H2) refines this scenario, positing that different plant species might maintain distinct litter environments to which arthropod abundances respond. Without regard to specific plant effects, seasonal changes in litter profiles (H3) can account for temporal patchiness in arthropod abundance. The ecosystem size hypothesis provides a mechanism for tree, species and seasonal effects. It links increasing food chain length with habitat availability and its heterogeneity.

In a Panamanian rainforest we sampled litter arthropods in quadrats located near (1 m) and far away (30 m) from the parent trunk of 93 tree individuals (to test the tree hypothesis) from 10 tree species (to test the species hypothesis) in the early wet season, when litter is deepest. To test for effects of seasonal changes of litter profiles, we then resampled 25 trees (i.e., five individuals from each of five species) in the late wet season, when climatic conditions are similar, but litter is shallowest.

We found weak support for all tree, species and seasonality hypotheses. With few exceptions, trees and species did not sustain different arthropod abundances, neither early nor late in the wet season. Collembola abundance increased late in the wet season, when litter is shallowest. Supporting the ecosystem size hypothesis, accumulated litter either due to trees, species and seasonality sustained higher predator abundance and higher predator to prey ratios.

Our results suggest that plants may account for detrital, brown, food web structure; but these effects are mostly through plant-based provision of structural support. This study adds to growing evidence relating the ecosystem size hypothesis to litter environments and suggest a framework to understand plant-based bottom-up forces in structuring litter communities.

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1. Introduction

Explaining the high patchiness in abundance of litter arthropod communities embedded in detrital brown food webs (BFWs) is an enduring challenge (Coleman, 2008). As primary producers, plants may shape BFW structure, defined here as the relative abundance of different arthropod taxa, by providing nutrients and habitat conditions required for litter arthropod survival (Finzi et al., 1998; Wardle, 2005; Moore et al., 2004; Castro and Wise, 2009; Bargett and Wardle, 2010). Previously, we demonstrated that mite and ant diversity (the number and identity of species) did not respond to plant identity in a tropical forest (Donoso et al., 2010). However, the general hypothesis that arthropod abundance can respond to tree identity remains unsolved. The tree hypothesis (TH), proposed here, posits that differences in litter profiles (e.g., in volume, structure or chemistry) between environments directly below tree canopies and those farther away may account for patchiness in arthropod abundance. If TH is true, the species hypothesis (SH) posits that plants, through interspecific differences in litter profiles which they maintain underneath their canopies, may account for patchiness in arthropod abundance (Bezemer et al., 2010). Thus, different plant species sustain different BFWs. Indeed, both tree and species effects have been reported in the literature. Specific plant

taxa (e.g., legumes) can support different microbial communities through differences in litter chemistry (Grayston et al., 1998; Bardgett et al., 1999). Plants are also known to affect the distribution of arthropod faunas feeding upon microbes and other arthropod groups (De Deyn et al., 2004; Barton et al., 2010).

Taking into account these two hypotheses, tropical plant effects on BFWs may be understood within a simple framework (Table 1): if both tree and species effects are present, then BFW structure might change strongly across the forest floor, reflecting tree species identity and distribution (Donoso et al., 2010). This scenario predicts patchiness in BFW structure to be tightly linked to plant diversity. In contrast, if neither species nor tree effects are present, then BFW structure will be independent of plant diversity and distribution, suggesting an absence of co-evolutionary processes between litter arthropods and the plants producing the litter habitat. If tree but not species effects determine BFW structure, this would suggest that litter plays a predominantly structural role, maintaining habitat heterogeneity necessary for arthropod survival, but not providing species-level clues that might affect arthropod distribution. Variability in responses of arthropod groups often encountered in litter addition experiments attests for this possibility (Sabo et al., 2005; Sayer et al., 2010). Finally, a scenario with species, but not tree effects, suggests that associations of BFW taxa to tree species are due to stronger effects of a third factor, such as soil nutrients or topography (Lessard et al., 2011).

In seasonal tropical forests litter production is variable (Cornejo et al., 1994; Wright and Cornejo, 1990; Williams et al., 2008) providing a temporal aspect to patchiness in arthropod distribution and BFW structure. For example, in Barro Colorado Island, Panama, litter fall is highest and decomposition rates are lowest in the 3-month dry season; litter fall is lowest and litter decomposition highest during the 9-month wet season (Windsor, 1990; Wright and Cornejo, 1990). Thus, there is a high abundance of structurally complex and nutrient-rich litter at the beginning of the wet season. Closer to the end of the wet season, most of this litter has been decomposed, leaving a thin layer of relatively homogeneous and recalcitrant litter. This seasonality in litter profiles may account for patchiness in arthropod abundance and have further implications for the relationship between plants and litter arthropod communities, proposed here as the TH and SH. In general, we expect tree and species effects on BFWs to be strongest at the start of the rainy season, when litter depth is highest.

While links between litter arthropods and plant species abound in the literature (see Bargett and Wardle, 2010 for a review), there is little consensus about the specific mechanisms behind the TH, SH, or

seasonal variation in arthropod community composition. The ecosystem size hypothesis (ESH; Cohen and Newman, 1991; Post et al., 2000; Post, 2002a; Kaspari and Yanoviak, 2009), often applied to aquatic systems (Takimoto et al., 2008; Doi et al., 2009; McHugh et al., 2010), provides one possible mechanism. It assumes that predators are space limited, and that larger ecosystems maintain stability and permanence of higher trophic levels (Cohen and Newman, 1991; Post et al., 2000). The ESH predicts an increase in food chain length, i.e., the number of trophic transfers from detritivores to top predators in a food web, with ecosystem size. At small scales, litter depth is a measure of ecosystem size in terrestrial ecosystems because it is correlated with the supply of both shelter and food to litter arthropods (Wardle et al., 2006). The area of sample quadrats in soil biodiversity studies (usually ≤ 1 m^2) provides good representations of ecosystem size because home ranges of litter arthropods are generally limited to a few square metres (Post, 2002a); e.g., in tropical forests most ant species forage within 1 m from its colony entrance (Kaspari, 1996). Because trophic food chain length is difficult to measure in litter ecosystems where diversity and abundance of organisms is noticeably high, we can then expect a higher ratio of predacious taxa to microbivores as litter volume increases (Post, 2002a; Kaspari and Yanoviak, 2009). If ESH is true, shallow patches of litter will be dominated by fungivore and detritivore taxa and depleted of predator taxa that are limited by space. There is evidence that the ESH shapes litter communities; e.g., in a geographic study across 26 forests, the predator to prey ratio of litter fauna increased with litter depth (Kaspari and Yanoviak, 2009). Furthermore, in an Ecuadorian montane forest, reduced habitat availability due to experimental nutrient addition increased litter decomposition and reduced predator abundances (Jacquemin et al., 2012). We thus posit that if trees or tree species differ in average litter depth maintained underneath their canopies or among seasons, then the ESH may provide a mechanism for the TH, SH and seasons, via litter depth's effect on BFW's trophic structure.

We tested the TH and the SH by measuring how tree individuals and tree species supported different arthropod taxa, thus contributing to the high patchiness in abundance of tropical litter arthropod groups. Second, we explored how arthropod groups responded to seasonality, one of the main generators of temporal variability in litter profiles within a forest. Finally, we used stable isotopes (δ^{15}N) of several major BFW taxa (sorted to class and order levels) to infer litter arthropod's trophic level and test the ESH as a mechanism generating higher predator to prey ratios under either tree individuals, tree species, or months with deeper litter.

2. Materials and methods

2.1. Study site

Research was conducted on the 50-ha plot (Hubbell, 2004; 09°06′ N; 79°50′ W) managed by the Center for Tropical Forest Science on Barro Colorado Island (BCI), Panama Canal Zone, Republic of Panamá. BCI is a 420-km^2 lowland seasonal moist forest with an average annual rainfall of 2600 mm and 27 °C average daytime temperature. The wet season usually lasts from June to December and the dry season, which normally brings less than 300 mm of rain of total annual rain, lasts from January to May. Tree diversity inside the plot is moderately high (301 species from >230,000 individuals with stems >1 cm diameter at breast height) compared to other tropical forests (Leigh et al., 2004).

2.2. Focal trees

Our ten target tree species were selected in the field to represent a gradient of chemical and structural variability encountered

Table 1
Working framework for possible scenarios of the tree and species hypotheses. Expected outcomes and mechanisms for associations between BFW structure and plants.

Tree hypothesis	Species hypothesis	
	True	False
True	BFW structure changes with proximity to the tree, and across tree species. Patchiness of BFW structure linked to tree diversity.	BFW structure changes with proximity to trees. Plants provide litter-based structural variability only.
False	Tree species and BFWs respond together to third factors (e.g., soil nutrients, topography).	No association. BFW structure is independent of plant and plant-based resources. Absence of interactions and coevolutionary processes.

among BCI tree species. We chose mature trees to maximize the area, magnitude and duration of that tree's impact on the local litter (Elger et al., 2009). We then maximized distance between individuals of the same species. We reported previously (Donoso et al., 2010) how these tree species modified four key litter traits known to influence BFW structure; briefly: 1) *litter depth*, measured from four corners of the arthropod sampling quadrat; 2) *litter fall footprint*, potential area being modified by the tree trunk; 3) *leaf species heterogeneity*, the ratio of focal vs. non-focal leaves contained in 0.25 m^2; and 4) *leaf chemistry* (% N, P, K, Mg, Ca, and measures of Phenolic, Tannin, Protein and Lamina Fracture). These traits reflected variability in resource quantity and quality provided by our focal tree species (Hansen and Coleman, 1998; Hansen, 2000; Kaspari and Yanoviak, 2009; Donoso et al., 2010).

2.3. Arthropod taxa

In June and July 2002, we sampled litter communities under a total of 93 tree individuals (8−10 individuals per tree species). Under each tree individual, we collected litter samples from two 0.25 m^2 quadrats located 1 m away at opposite sides of the trunk. We averaged the two samples collected in near quadrats (i.e., 1 m away from the parent trunk) to provide a better representation of arthropod abundance under every tree individual sampled. A third sample taken from a 0.25 m^2 quadrat located 30 m away from the trunk in a random direction measured local effects beyond the tree canopy. To measure the effect of seasonality on litter communities we re-sampled, in November 2002, 25 tree individuals from five target tree species. In November, we took two litter samples from 0.25 m^2 quadrats, located 1 m and 30 m away from each parent trunk. The leaf litter was sifted through 1-cm mesh and the siftate from all samples was hung for 48-h in a mini-Winkler extractor.

We focused on eight common litter arthropod groups spanning through most trophic levels of BFWs (except microbes) and roles in ecosystems: oribatid mites (Acari: Oribatida), predatory mites (Acari: Mesostigmata; but individuals of Trombidiidae and Prostigmata may have been included in this group), spiders (Araneae), ants (Hymenoptera: Formicidae), rove beetles (Coleoptera: Staphylinidae), pill bugs (Isopoda), springtails (Collembola) and millipedes (Diplopoda) (Coleman et al., 2004). Some of these taxa are usually regarded as mesofauna (mites, springtails) and affect litter decomposition by ingesting and comminuting it. Groups such as ants and spiders are considered macrofauna and participate as main predators and ecosystem engineers (Coleman et al., 2004). We characterized the trophic level of our eight target arthropod taxa using nitrogen (N) stable isotope values (δ^{15}N). Stable isotope analysis provided a powerful tool to explore the nature and extent of trophic relationships between and within BFWs; known to consist of species rich, trophically complex and functionally diverse arthropod groups (Post, 2002b; Illig et al., 2005). Protocols for stable isotope quantification were detailed in Supplement Material 1.

2.4. Seasonality in litter depth

Litter depth was measured from four corners of all the arthropod sampling quadrats in June and November. To test for seasonal changes of litter profiles, we ran a linear model, using tree species as main treatment and both distance to parent trunk (near vs. far plots) and month (June and November) as covariates.

2.5. Testing the tree hypothesis and its seasonality

The TH assumes that litter arthropod abundance is variable among the forest floor and that tree effects, regardless of species identity, are greater directly underneath the trunk, than far away. It predicts that BFW structure will respond to proximity to tree trunks. We used a Negative Binomial GLM (i.e., a specific version of a Poisson model that uses an additional parameter to correct for data over-dispersion), with a log link function to compare the densities of taxa in near vs. far plots (distance treatment) and between June and November (seasonality treatment). Negative Binomial GLMs are designed to fit count data (data that usually that lacks normality), as it is generally the case when sampling invertebrate taxa in quadrats (Sileshi, 2006). We used a Chi-Square test (X^2) to test the general hypothesis that our treatments (Distance and Seasonality) have a significant explanatory power. When multiple comparisons were done, significance was assessed after Bonferroni corrections. We used R v.2.13.1 (R Development Core Team, 2011) using the "MASS" (Venables and Ripley, 2002) and "lmtest" (Zeileis and Hothorn, 2002) packages.

2.6. Testing the species hypothesis and its seasonality

The SH assumes that individual trees can influence arthropod abundance and that litter profiles are variable across tree species. It predicts that arthropod abundance is variable among tree species. Similarly to the approach given to the TH, we tested for the SH using Negative Binomial GLM. In the model, we only included samples collected near the parent trunk to test for differences in arthropod abundance across tree species. Tree species served as the different levels of this analysis. As before, we also explored seasonality effects of litter profiles by including June and November samples in the model as a second treatment.

2.7. Testing the ecosystem size hypothesis

The ESH assumes that predator taxa are largely constrained by habitat space. It predicts that food chain length in the system should increase with ecosystem size. As a proxy for food chain length, i.e., total number of trophic levels from herbivores to top predators, we used predator to prey ratios. Assignment of different arthropod taxa to predator or prey categories was confirmed through stable isotopes analyses (Supplementary Material 1). First, we performed linear regressions of predator abundance, prey abundance and predator to prey ratios with litter depth for both June and November samples. To test for the ESH as a mechanism for the TH, we explored the effects of distance to the parent trunk on predator abundance, prey abundance and predator to prey ratios. To test for the ESH as a mechanism for the SH, we explored the effects of tree identity on predator abundance, prey abundance and predator to prey ratios. We conducted these analyses using General Lineal Models, and present analyses conducted separately for June and November.

3. Results

3.1. Focal arthropod taxa

In June, in quadrats closest to parent trunks, we collected a total of 7856 specimens from our 8 focal arthropod taxa (Table SM2). Formicidae and Oribatida were the most abundant taxa with 2627 (33.44%) and 2809 (35.76%) individuals, respectively. Araneae and Isopoda, with 193 (2.46%) and 181 (2.3%) individuals, were the least collected taxa.

3.2. Seasonality in litter profiles

Litter depth varied significantly across tree species ($F = 5.87$, df $= 9$, $p < 0.001$), distance (near vs. far plots, $F = 34.32$, df $= 1$, $p < 0.001$), and time of season (June vs. November, $F = 24.19$, df $= 1$,

$p < 0.001$). Interaction effects between tree species and distance were significant ($F = 4.04$, df = 9, $p < 0.001$), but they were not among tree species and month of sampling ($F = 1.93$, df = 4, $p = 0.106$).

3.3. Stable isotope analyses

$\delta^{15}N$ values from our eight common taxa ranged from an average of 4.1‰ for Oribatida to 9.02‰ for Mesostigmata (Fig. SM1). Based on the assumption of an enrichment of 3.4‰ per trophic level, we suggest that arthropods in our collection site can be arranged in two trophic levels, primary consumers (i.e., prey) and predators. However, ANOVA and Tukeys HSD analysis suggested the presence of three independent groups (ANOVA, $F_{7,72} = 43.51$, $p < 0.001$). The lower trophic level (fungivores and detritivores) is composed of collembolans, diplopods, oribatids and isopods. The second trophic level (omnivores) includes only the rove beetles. The third trophic level (predators) is composed of ants, mesostigmatids and arachnids (Fig. SM1). We grouped seven arthropod taxa (excluding rove beetles) in predator and prey categories using these divisions.

3.4. Testing the tree hypothesis and its seasonality

We did not find strong support for the tree hypothesis. Trees alone (without regard to its specific identity) influenced only marginally the arthropod abundance underneath their canopy. Only the abundance of arachnids (Negative Binomial GLM, Distance, $X^2 = 7.7$, $p = 0.005$) was higher in near (1 m) vs. far (30 m) plots. Seasonal effects, however, were marked with the abundance of most groups decreasing in November, when litter is shallowest. Only the abundance of Collembola increased in November (Tables 2 and SM2).

3.5. Testing the species hypothesis and its seasonality

In partial support for the species hypothesis, the abundance of arachnids (Negative Binomial GLM, Distance, $X^2 = 23.1$, $p = 0.006$) and isopods (Negative Binomial GLM, Distance, $X^2 = 30.2$, $p < 0.001$) differed across combinations of tree species (Tables 2 and SM2). Detailed results revealed that abundance of arachnids was significantly lower in *Astroniun* and *Proteum* trees (results not shown). Isopoda abundance was significantly higher in *Anacardium*, *Dendropanax* and *Cordia* trees (results not shown). Abundances of most arthropod groups among tree species decreased in November, except Collembola, which presented the opposite trend (Tables 2 and SM2).

3.6. Ecosystem size hypothesis and tree hypothesis

In June, in partial support for the TH and ESH, we found significant tree effects and near (1 m away) quadrats hosted significantly more predators (Distance, $F_{1,181} = 5.15$, $p = 0.027$) and marginally less prey (Distance, $F_{1,181} = 3.03$, $p = 0.084$) (Table 3). However, predator to prey ratios did not increase in deeper litter in near quadrats. In November, when litter depth across the forest floor is shallowest and most homogeneous, prey abundance increased in near quadrats (Distance, $F_{1,66} = 6.98$, $p = 0.010$). Consequently predator to prey ratios were lower in near quadrats as compared with far quadrats (Distance, $F_{1,66} = 5.92$, $p = 0.018$) (Table 3).

3.7. Ecosystem size hypothesis and species hypothesis

In June, tree identity did not account for the abundance of predators, prey and predator to prey ratios (Table 3). In November,

Table 2
Testing the species (SH) and tree (TH) hypothesis. Results of the negative binomial GLM regression for eight common arthropod taxa. The model for testing TH included distance and month as treatments. The model for testing SH included tree identity and month as treatments. Interaction effects were removed from models due to their overall non-significance. Values in **bold** are significant after Bonferroni correction ($p = 0.05/8 = 0.006$).

	Tree hypothesis				Species hypothesis		
	X^2	df	p		X^2	df	p
Aranea							
Distance	7.7	1	**0.005**	Identity	23.1	9	**0.006**
Month	75.0	1	**<0.001**	Month	19.9	1	**<0.001**
Collembola							
Distance	3.5	1	0.062	Identity	12.1	9	0.210
Month	16.3	1	**<0.001**	Month	19.5	1	**<0.001**
Diplopoda							
Distance	0.1	1	0.766	Identity	8.5	9	0.486
Month	45.5	1	**<0.001**	Month	22.5	1	**<0.001**
Formicidae							
Distance	5.2	1	0.023	Identity	16.7	9	0.053
Month	63.5	1	**<0.001**	Month	32.1	1	**<0.001**
Mesostigmatids							
Distance	3	1	0.068	Identity	7.4	9	0.599
Month	10.8	1	**0.001**	Month	2.0	1	0.162
Isopoda							
Distance	1.0	1	0.325	Identity	30.2	9	**<0.001**
Month	14.1	1	**<0.001**	Month	6.7	1	0.009
Oribatids							
Distance	2.3	1	0.131	Identity	18.4	9	0.031
Month	44.0	1	**<0.001**	Month	17.5	1	**<0.001**
Staphylinid							
Distance	0.5	1	0.485	Identity	10.7	9	0.299
Month	24.6	1	**<0.001**	Month	9.0	1	**0.003**

only the abundance of predators varied across tree species (Tree spp., $F_{4,28} = 3.70$, $p = 0.015$). Tukeys HSD comparisons (data not shown) revealed that *Anacardium* trees, which supported the deepest litter, drove these interspecific comparisons.

3.8. Ecosystem size hypothesis and seasonality hypothesis

The ESH predicts a proportional increase in the relative proportion of predators and litter depth. In June, when litter depth is highest, linear regressions showed significant increases in predator taxa ($R^2 = 0.22$, $p < 0.001$) and in the predator to prey ratio ($R^2 = 0.13$, $p < 0.001$). In November, when litter depth is shallowest and more homogeneous, predator ($R^2 = 0.34$, $p < 0.001$), prey taxa ($R^2 = 0.20$, $p < 0.001$), and less strongly (but still significant) the predator to prey ratio ($R^2 = 0.16$, $p < 0.012$) accumulated on deeper litter (Fig. 1).

4. Discussion

There is growing evidence that plants modify arthropod distribution (Barton et al., 2010; Bargett and Wardle, 2010) and BFW structure, but there is less certainty about the mechanisms behind these patterns. The framework we present here identifies two different pathways by which plants can account for arthropod distribution. Trees can modify BFW structure if they maintain a different environment under their canopies. We tested specific predictions of litter effects on BFW structure across three natural gradients (across species, between species, and temporally) in a 50 ha tropical plot. Our results suggest that in seasonal tropical forest, both trees and seasonality, through their effects on litter depth (e.g., a measure of ecosystem size), shape the distribution of different litter taxa and modify the relative proportion of predators to prey (e.g., a measure of food chain length), modifying trophic structure of detrital BFWs, across the forest floor.

Table 3
Testing the ecosystem size hypothesis as a mechanism for the tree and species hypotheses. Results of GLMs for predator abundance, prey abundance and predator to prey ratios. The models included distance to the parent trunk (tree hypothesis) and tree species (species hypothesis) as treatments. Values in **bold** are significant at $p = 0.05$.

		June				November			
		Sq. sum	df	F	p	Sq. sum	df	F	p
Tree hypothesis									
Predator	Distance	2.39	1	5.15	**0.027**	0.66	1	0.83	0.366
	Residuals	87.47	181			52.67	66		
Prey	Distance	1.82	1	3.03	0.084	5.45	1	6.98	**0.010**
	Residuals	109.39	181			51.47	66		
Predator:Prey	Distance	0.44	1	0.55	0.454	1.38	1	5.92	**0.018**
	Residuals	141.50	181			15.36	66		
Species hypothesis									
Predator	Tree spp.	1.98	9	0.50	0.868	9.34	4	3.70	0.015
	Residuals	37.09	85			17.66	28		
Prey	Tree spp.	1.18	9	0.28	0.980	4.57	4	2.22	0.914
	Residuals	40.27	85			14.34	28		
Predator:Prey	Tree spp.	2.66	9	0.71	0.694	0.36	4	1.87	0.144
	Residuals	35.29	85			1.34	28		

Trees influenced BFW taxa, but their effects were mostly independent of tree species identity. For example, individual tree species did not support different target arthropod groups. Exceptions to this pattern were mostly found with Collembola and Isopoda, with varying abundance under *Anacardium*, *Virola* and *Cordia* trees. We suggest at least three reasons why. First, the litter below individual trees is still heterogeneous—a single m^2 on BCI may receive inputs from 30 tree species (Joseph Wright, pers. comm.). Arthropods looking for environments shaped by a permanent set of chemical variables may have difficulties finding such places, either due to the rareness of areas that meet their requirements or because high plant productivity and decomposition rates can modify litter environments relatively quickly. Second, the high rainfall in tropical forests is likely to promote rapid leaching of litter (leaf, flowers, fruits) nutrients, leaving behind only litter material that is chemically homogeneous but structurally complex (Luo and Zhou, 2006). Third, most litter arthropods are separated from plants by at least one trophic level, i.e., microbes. Thus microbes,

but not litter arthropods, are expected to coevolve with plant materials (Bargett and Wardle, 2010). Clearly, there is a paucity of information on the possible clues that would allow individual tree species to become templates of BFW diversification.

While individual tree species had almost no influence on BFWs structure, litter depth explained the abundance of several arthropod groups (e.g., Formicidae, Mesostigmata and Staphylinidae and to a lesser extent, Diplopoda and Araneae) and predator to prey ratios. These results are consistent with the ESH and contrast with previous work (Castro and Wise, 2010; Bezemer et al., 2010) that found litter quality and not quantity to be the main driver of differences in community structure (but see Scheu and Falca, 2000). Moreover, our results may explain in part the lack of response of higher trophic levels to experiments of bottom-up limitation (Scherber et al., 2010; Lessard et al., 2011) that do not modify habitat size.

A missing link in our study is the response that microbial communities (fungal and bacterial) may have to litter of different
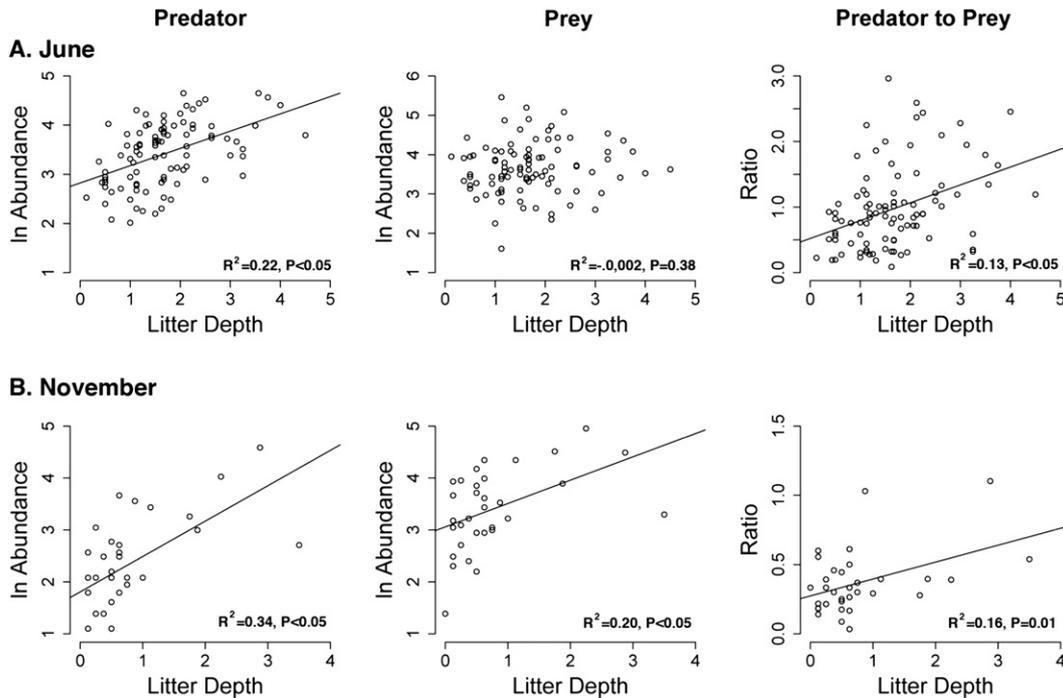

Fig. 1. Linear regressions of litter depth against predator abundance, prey abundance and predator [in ln(X + 1) scale] and prey ratios in June and November.

tree species and seasons. Microbes are both the main decomposers of leaf litter and the main food source at the base of detrital brown food webs. As such, microbes may mediate and shape any plant–soil–arthropod interaction in essential ways. For example, diversity of soil arthropods in lower trophic levels may be directly related to the level of resource specialization of microbivores. If this is the case, indices of microbial specialization to detrital resources, currently unknown, should be exciting venues in future research (Coleman, 2008).

Seasonality also explained patchiness in trophic structure of BFWs across the 50 ha plot. In June, predator abundance and predator to prey ratios, but not prey abundance, increased with litter depth. In contrast, in November, when litter depth was more shallow and homogeneous, both predator and prey abundance, but not predator to prey ratios, increased with litter depth. These results suggest that increases in predator number and predator to prey ratios result from either (1) transfer of biomass from lower trophic levels to higher ones —that is, predators limiting the size of prey population (Milton and Kaspari, 2007); or (2) an attraction effect—that is, predators are attracted to deep litter, but do not start top-down trophic cascades. Together these results give further support to the ESH and suggest that a minimum habitat volume is needed to host litter arthropods, regardless of their trophic level. Alternatively, these data suggest that there may be a threshold effect where, in deep enough litter, predators can control the density of their prey (Osler et al., 2006; Kaspari and Yanoviak, 2009).

Together, our results suggest for the first time in a seasonal tropical forest that plant-based and season-based changes in litter depth are of importance to predator taxa (Uetz, 1979). Litter depth dynamics may shape the structure and patchiness of BFWs at small spatial scales. Studies of arthropod effects on ecosystem processes would benefit by independently modifying nutrient availability (bottom up) and/or predator numbers (top down) with ecosystem size (e.g., Shik and Kaspari, 2010).

Acknowledgements

Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.02.004.

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