

Trees as templates for tropical litter arthropod diversity

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Abstract Increased tree species diversity in the tropics is associated with even greater herbivore diversity, but few tests of tree effects on litter arthropod diversity exist. We studied whether tree species influence patchiness in diversity and abundance of three common soil arthropod taxa (ants, gamasid mites, and oribatid mites) in a Panama forest. The tree specialization hypothesis proposes that tree-driven habitat heterogeneity maintains litter arthropod diversity. We tested whether tree species differed in resource quality and quantity of their leaf litter and whether more heterogeneous litter supports more arthropod species. Alternatively, the abundance–extinction hypothesis states that arthropod diversity increases with arthropod abundance, which in turn tracks resource quantity (e.g., litter depth). We found little support for the hypothesis that trop-

ical trees are templates for litter arthropod diversity. Ten tree species differed in litter depth, chemistry, and structural variability. However, the extent of specialization of invertebrates on particular tree taxa was low and the more heterogeneous litter between trees failed to support higher arthropod diversity. Furthermore, arthropod diversity did not track abundance or litter depth. The lack of association between tree species and litter arthropods suggests that factors other than tree species diversity may better explain the high arthropod diversity in tropical forests.

Keywords Tree specialization hypothesis · Abundance · Leaf litter · Arthropods

Introduction

Tropical forests occupy 11% of the earth's surface yet maintain more than 60% of its terrestrial biodiversity (Erwin 1982; Stork 1988). Many theories have been proposed to explain the relatively high species richness of insects in tropical forests (Anderson 1975; Basset 1992, Bardgett et al. 2005b; Novotny et al. 2006). One, which we call the tree specialization hypothesis (TSH), a specific version of niche theory derived from Erwin's (1982) work, posits that tropical arthropod diversity can be explained, at least in part, by arthropod specialization to a limited number of tropical tree taxa. If such, greater tree diversity in the tropics is expected to sustain an even greater arthropod diversity (May 1988; Novotny et al. 2006, 2007; Lewinsohn and Roslin 2008). Most tests for this hypothesis come from aboveground herbivore arthropods (e.g., coleopterans and lepidopterans).

Litter arthropods are mostly members of the detritus-based “brown” food web (BFW). BFWs are responsible for

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the recycling of nutrients and releasing the energy locked in all plant tissues (Coleman et al. 2004; Bardgett 2005, Bardgett et al. 2005a). They also constitute half or more of arthropod diversity in a tropical forest (Stork and Grimbacher 2006). Litter arthropods are assumed to be generalists because leaf litter and litter arthropods do not coevolve (Scheu and Setälä 2002; Wardle 2005; Ayres et al. 2006). Unlike aboveground herbivore assemblages (Coley and Barone 1996), litter arthropods do not interact directly with living plants, but harvest nutrients from dead plant material and the microbes decomposing the litter (Seastedt 1984; Moore et al. 1988). Nonetheless, the extent to which litter arthropods in BFWs conform to the TSH remains largely untested (André et al. 1994, 2002; Yanoviak and Kaspari 2000; St. John et al. 2006; but see Maraun et al. 2007).

To apply to BFWs, the TSH must meet two requirements (Tilman and Pacala 1993; Rosenzweig 1995). First, the environment must be heterogeneous in ways important to litter organisms. Variability in climate and soil nutrients impacts arthropod dynamics at large geographic scales (Townsend et al. 2008). At local scales (<1 km²), habitat heterogeneity on the soil surface may be expressed as differences in traits of the plant species contributing to the litter pool, including food (e.g., palatable leaf litter, fruits, seeds, and herbivore frass), toxins, (e.g., phenols and tannins) and structural complexity that creates habitat (e.g., branches, twigs, and leaf litter depth) (Kaspari 1993; Dominy et al. 2003; Williams et al. 2008). However, little is known of the influence that tree-driven litter heterogeneity has on the abundance and diversity of tropical litter arthropods (Anderson 1978; Kaspari 1993; Giller 1996; Scheu 2005; St. John et al. 2006).

Second, the TSH requires that litter taxa have adaptations to the litter of different tree species that allow those taxa to increase even when rare (Hutchinson 1959). In BFWs, a variety of functional groups may meet this assumption. These include saprophytic arthropods that feed directly on dead plant tissue (Illig et al. 2005; Scheu 2005); and arthropods that consume seeds, pollen and fruits (e.g., several ant genera and bruchid seed beetles; Kaspari 1993, 1996; Jermy and Szentesi 2003; Wilson 2005). For example, experiments have linked litter heterogeneity and composition to mite (Hansen and Coleman 1998; Hansen 2000) and ant (Armbrrecht et al. 2004) diversity. A wide range of microbivores, one trophic level removed from plant consumers, may also specialize if the microbes themselves differ among tree species (Grove 2002). Nevertheless, a prevailing view suggests that BFWs are composed of functionally redundant taxa consuming the same nutrient rich, but recalcitrant, leaf litter (Scheu and Setälä 2002; but see Illig et al. 2005; Scheu 2005; Wilson 2005) even as microbial decomposition further homogenizes, i.e. humifies, the

litter's chemical and physical profile (Bardgett and Cook 1998; Setälä et al. 2005).

A second way for trees to shape BFW diversity is that, if tree species differ in the amount of resources flushed to the environment, then tree species may accumulate more arthropod species (S) simply because they accumulate more arthropod individuals (N) (May 1975; Kaspari et al. 2003). This can happen for two, related reasons. First, as a patch attracts more arthropods, it will be increasingly likely to accumulate rare species, increasing S (the sampling hypothesis; Kaspari et al. 2003). Second, at larger spatial scales, highly productive patches may prevent rare species from going locally extinct, preserving higher S (the abundance extinction hypothesis; Hubbell and Foster 1986; Kaspari et al. 2003). Both hypotheses predict a positive, decelerating curve of S with N, but can be distinguished by plotting Fisher's alpha (a diversity index that removes sampling effects) with N.

Here, we explore how the species of three common litter arthropod taxa are distributed under ten tree species in a Panama rainforest at local scales (<1 km²). First, we investigated the extent of the variability in four tree traits (litter depth, litter chemistry, leaf species heterogeneity, and litter fall footprint) of known importance to litter arthropods among the tree species. We then tested the TSH by assaying the extent of specialization of the arthropod groups to the tree species and by investigating whether more heterogeneous litter sustains more diverse arthropod assemblages. Finally, we test the alternative hypothesis that arthropod abundance promoted arthropod diversity across tree species that differed in the amount of resources flushed to the environment.

Materials and methods

Focal taxa

We focused on three common litter arthropod groups: oribatid mites (Acari: Oribatidae), gamasid mites (Acari: Gamasidae), and ants (Hymenoptera: Formicidae). These arthropod groups differ in important traits and roles in ecosystems, such as size and diet (Walter and Proctor 1999). Oribatid mites are an abundant and diverse group of microbivorous micro-arthropods, which are specialized on microbes and dead plant tissues and aid in the comminuting of plant litter (Hansen 2000; Illig et al. 2005). Gamasids are mostly predatory mites that use a specialized proboscis to pierce the integument of other small micro-arthropods (Illig et al. 2005). Ants are part of the soil macrofauna and are important predators (Wilson 2005) and ecosystem engineers via their tunneling through soil (Jouquet et al. 2006).

Locality description

Research was conducted on the Center for Tropical Forest Science (CTFS) 50-ha plot (Hubbell 2004), on Barro Colorado Island (BCI) in the Panama Canal Zone, Republic of Panamá (09°06'N, 79°50'W). BCI is a 420-km² lowland seasonal moist forest (2,400 mm average annual rainfall and 18°C average daytime temperature). The wet season usually lasts from June to December and the dry season from January to May. Topographically, the plot is relatively flat, located on the island's basalt cap. Tree diversity inside the plot is moderately high compared to other tropical forests: an inventory of all free-woody stems ≥ 1 cm diameter at breast height (DBH) on the plot counted 301 species from ~230,000 individuals (Leigh et al. 2004).

Trees create heterogeneity in litter environment

We collected arthropods under 10 tree species (Table 1), which were selected from the literature to represent most of the chemical variability encountered among Barro Colorado forest trees and summarized under five functional groups: +tannin; +lignin; +tannin and +lignin; +calcium; and +palatability (Coley 1983; Dominy et al. 2003). We selected mature trees of maximal DBH to maximize the size and duration of that tree's impact on the local litter (Elger et al. 2009), secondarily maximizing distance between individuals of the same species.

For each tree species, we measured heterogeneity in four litter features known to influence BFW structure (Hansen and Coleman 1998; Hansen 2000; Armbrrecht et al. 2004; Kaspari and Yanoviak 2008). *Litter depth* was measured from four corners of the arthropod sampling quadrat (see below). Each tree individual's *litter fall footprint* was measured, in June 2002, by laying out a transect in a random direction, skewering litter every 1 m, and counting the number of collected focal leaves. We ended sampling when no leaves from the focal species were discovered for 5 m.

Litter chemistry was measured at the end of the dry season in April 2003. Newly fallen leaves were gathered from under each target tree individual to analyze % N, P, K, Mg, Ca. As newly fallen leaves were rare, leaves of conspecifics were pooled together for a single analysis. Samples were frozen and cleaned of epiphytes and fungi, subsequently air-dried and sent for chemical composition analysis to the Oklahoma State Soil, Water, and Forage Analytical Laboratory (OSU 2009). Phenolic, tannin, protein, and Lamina Fracture levels for each tree species were gathered from Dominy et al. (2003). *Leaf species heterogeneity* (no. of leaf species contained in 0.25 m²) was measured 1 and 30 m away from each tree individual in a random direction in June 2003. A 0.25-m² quadrat was placed on the litter, and the number of focal and non-focal species leaves estimated within that quadrat.

We used one-way ANOVA to test for differences in litter fall footprint on the soil surface and litter heterogeneity in near versus far plots. We used ANCOVA, with tree identity as covariate, to test for differences in litter depth underneath the ten tree species. To summarize and describe the variability in litter chemistry among tree species we used principal components analysis (PCA; Jolliffe 2002). These analyses were performed using the statistical software package R (R Development Core Team 2008).

Arthropod sampling and identification

In June and July 2002, we sampled oribatids, gamasids, and ants under a total of 93 individuals on 10 target tree species (Table 1). Two litter samples were taken from two 0.25 m² quadrats located 1 m away at opposite sides of the trunk. A third sample taken from a 0.25-m² quadrat located 30 m away from the trunk in a random direction measured local effects beyond the tree canopy. Leaf litter was collected down to mineral soil and sifted through 1-cm mesh. The siftate was hung for 48 h in a mini-Winkler extractor (Agosti et al. 2000). Winkler sampling is considered to be

Table 1 Characteristics of ten Neotropical tree species sampled in this study within the 50-ha CTFS plot

No.	Code	Family	Species	Syndrome	Number of trees	Litter depth (cm)
1	ALco	Euphorbiaceae	<i>Alchornea costaricensis</i>	+palatability	10	1.61
2	ANex	Anacardiaceae	<i>Anacardium excelsum</i>	+tannin; +lignin	10	3.46
3	ASgr	Anacardiaceae	<i>Astronium graveolens</i>	+tannin	9	1.39
4	CEob	Cecropiaceae	<i>Cecropia obtusifolia</i>	+palatability	10	1.22
5	COal	Boraginaceae	<i>Cordia alliodora</i>	+calcium	10	1.25
6	DEar	Araliaceae	<i>Dendropanax arboreus</i>	+lignin	9	1.18
7	PRte	Burseraceae	<i>Protium tenuifolium</i>	+tannin; +lignin	9	2.04
8	TAve	Fabaceae	<i>Tachigali versicolor</i>	+calcium	9	2.86
9	TRmi	Ulmaceae	<i>Trema micrantha</i>	+lignin	8	0.94
10	VImu	Myristicaceae	<i>Virola multiflora</i>	+tannin	9	1.8

Tree species were assigned to one of five chemical syndromes with possible influence on arthropods

an efficient, passive method for sampling litter arthropods (Donoso and Ramón 2009). Oribatids, gamasids, and ants were sorted to species/morphospecies level. We identified ants using standard taxonomic keys. Dr. Heinrich Schatz identified mites. All specimens were deposited in the collection of M.K. at the University of Oklahoma.

In most analyses, we pooled together the two samples collected in near quadrats (i.e. 1 m away from the parent trunk) to provide a better representation of species composition under every tree individual sampled. However, when we compared near (1 m) versus far (30 m) assemblages (see below), we selected randomly one of the two quadrats at 1 m. We quantified differences in the assemblage structure of gamasid, oribatids, and ants among individual trees and species using two metrics: the abundance of arthropod individuals and the number of arthropod species. We determined the degree of completeness of our sampling using species accumulation curves and estimated the species richness of our three arthropod taxa for each tree species using Fisher's Alpha implemented in the software program EstimateS (Colwell 2006).

Testing the tree specialization hypothesis (TSH)

The TSH assumes that litter species specialize on differing tree species. We used Indicator Values (IndVal) (Software IndVal 2.0, Dufrêne and Legendre 1997; Stork and Grimbacher 2006) to quantify this specialization. IndVal measured both the specificity (uniqueness to a tree species) and fidelity (frequency within that tree species) of a given arthropod taxon recorded in the survey. A high IndVal reflects high specificity and fidelity of a the arthropod species to a tree species (Dufrêne and Legendre 1997). The statistical probability to find a given IndVal for each arthropod species by chance alone was determined by 5,000 randomizations (Dufrêne and Legendre 1997). Differences were considered significant if $P < 0.05$. To calculate IndVals we use only data of arthropods collected underneath tree canopies (i.e. we excluded data from 30 m distance quadrats). For gamasids, oribatids we performed the analysis in an abundance matrix. For ants, living in colonies, we performed the analysis in a presence–absence matrix. Since the IndVal will be highest when the arthropod species occurs in all tree individuals from a given tree species and only in them, we restricted species included in this analysis to only those recorded by more than eight individuals (for mites) and eight species records (for ants), as this was our smaller sample size for some tree species.

We next tested the assumption that arthropod assemblages sampled from the same tree species were more similar than those recovered from other tree species, using non-metric multidimensional scaling (NMDS). We performed the NMDS ordinations in R v.2.8.1 (R Development Core

Team) using the Vegan package (Oksanen et al. 2005). NMDS is an ordination technique that represents samples as points in low-dimensional space, such that the relative dissimilarity of among samples were depicted by the relative distances separating them in a two-dimensional space (van der Gucht et al. 2005). We performed these analyses using arthropod abundance data. The Bray-Curtis method was used as a measure of similarity. To assess the similarity of arthropod assemblages among tree individuals, we used the NMDS goodness of fit R^2 and a stress function (which ranges from 0 to 1) where values < 0.2 suggested that ordination accurately represents the dissimilarity among samples.

The difference in composition of arthropod assemblages among tree species was tested using analysis of similarities (ANOSIM; Chapman and Underwood 1999). ANOSIM tests the null hypothesis that within-tree similarity in arthropod assemblage composition equals between-tree similarity. ANOSIM provides a test statistic R , with values close to 1 meaning dissimilarity among groups. Monte-Carlo randomization, using tree species as group labels, was used to test the hypothesis that within-group similarities were higher than would be expected by chance alone. The significance was assessed using a P value (Bonferroni corrected) of 0.05. We further performed pairwise ANOSIM comparisons between all pairs of tree species. ANOSIM analyses were performed using the statistical software PAST (Paleontological statistics, v.1.79).

Finally, TSH predicts that increasing litter heterogeneity should increase arthropod diversity. We evaluated this prediction by assessing the extent to which the more homogeneous litter underneath individual trees had consistently fewer species than the more heterogeneous litter 30 m away. For this analysis, we selected randomly one of the two near (1 m) arthropod samples before comparison with 30 m quadrats. To measure the extent to which litter arthropods respond to litter heterogeneity, we used an ANCOVA with tree species as covariate.

Testing the abundance–extinction hypothesis

The abundance–extinction hypothesis predicts that litter arthropod abundance is variable among tree species and is correlated with arthropod diversity, even after controlling for the sampling effect. It assumes that variability in litter depth across tree species may generate gradients of total gamasid, oribatid, and ant abundance across the forest floor. To test this hypothesis, we correlated litter arthropod diversities S (through Fisher's Alpha) with litter arthropod abundances N , under tree individuals. We further explored the correlation between litter arthropod diversity and litter depth under our target tree species.

Results

We collected, in pooled quadrats at 1 m, a total of 5,060 specimens and 35 species of oribatid mites. The most abundant oribatid (sp. 147) represented 29.5% of specimens. 20% of oribatid species ($n = 7$ species) were found under all 10 trees species (Fig. 1). Gamasid mites were rarer ($n = 708$) and represented 14% of all mites. Gamasid mites, with 62 morphospecies, were more diverse than oribatids. The most abundant gamasid (sp. 117) represented 24% of specimens; only 4.8% of gamasid species ($n = 3$ species) were found under all 10 trees species. We collected a total of 7,674 ants representing 93 species/morphospecies. The most abundant species (*Wasmannia auropunctata*) represented 8% of the specimens; 18.2% of ant species ($n = 17$ species) were found under all 10 tree species.

Species accumulation curves of litter arthropods under most tree species tended to stabilize and presented decreasing standard deviations with sampling effort. For ants, species accumulation curves stabilized on 6 of 10 tree species. For gamasids, species accumulation curves stabilized on 5 of the 10 tree species. For oribatids, species accumulation curves stabilized on 9 of the 10 tree species (Table 2). Different tree species supported the highest abundance and diversity of our three focal arthropod taxa. *Dendropanax arboreus* yielded the highest ant abundance per sampled tree individual ($n = 72$ N/individual), and ant species richness per sampled tree individual ($n = 15.1$ S/individual), and total expected ant species (Fisher's Alpha = 12.3) (Table 2). *D. arboreus* also supported the highest abundance of oribatids ($n = 107.0$ N/individual) but ranked tenth in expected species richness (Fisher's Alpha = 4.7) *Cecropia obtusifolia* supported more observed ($n = 6.9$ S/individual),

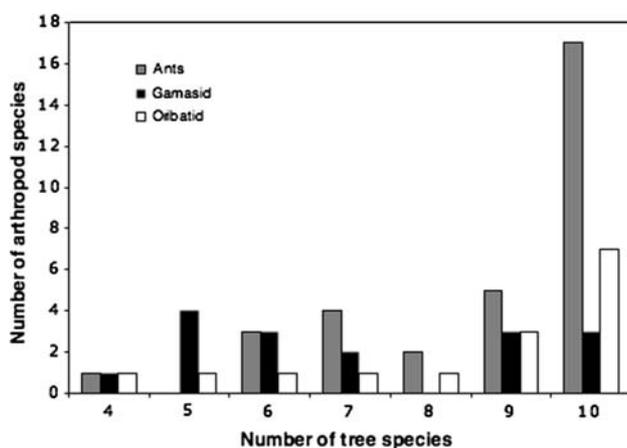


Fig. 1 Occurrence of arthropod taxa across tree species. Bars demonstrate the number of arthropod species found under a given number of tree species. Up to 22 ant, 6 gamasid, and 10 oribatid species were widespread, and were found under 9 or 10 of the tree species sampled. We restricted species included in this graph to only those recorded by more than 8 individuals (for mites) and 8 species records (for ants)

and expected richness (Fisher's Alpha = 5.4) of oribatids. Gamasid abundance was highest in *Alchornea costarri-cense* ($n = 8.7$ N/individual), and expected diversity (Fisher's Alpha = 14.5); but gamasid species richness was highest in *Cordia Alliodora* ($n = 4.6$ S/individual).

Trees create heterogeneity in litter environment

Significant differences existed among sampled tree species for all measured variables. Trees species differed in their litter fall footprint (ANOVA $F_{9,56} = 4.281$, $P < 0.001$) (Fig. 2). Leaves of *Alchornea costarri-censis* fell nearest to the parent trunk ($5.5 \text{ m} \pm 2.66$) whereas leaves of *Astro-nium graveolens* fell further from the trunk ($12.33 \text{ m} \pm 4.99$). Litter depth 1 m from the trunk varied threefold across tree species (ANOVA, $F_{9,77} = 5.01$, $P < 0.0001$) with *Anacardium excelsum* producing the deepest litter (6.2 cm) and *Trema micrantha* the shallowest (2.0 cm). Litter was consistently deeper beneath the canopy than in samples 30 m away (ANCOVA, $F_{1,140} = 12.90$, $P < 0.001$, tree \times distance interaction, $F_{19,140} = 1.41$, $P = 0.189$). Litter heterogeneity (no. of leaf species contained in 0.25 m^2) was consistently higher by almost two-fold in samples 30 m from the trunk (ANOVA, $F_{1,97} = 54.96$, $P < 0.001$) regardless of species (ANOVA $F_{4,97} = 1.18$, $P = 0.32$; tree \times distance interaction, $F_{9,97} = 1.16$, $P = 0.33$). The pooled litter samples also suggested considerable variability in leaf litter chemistry, as expected when these species were selected. For example, a 1.8-fold variation in N concentration, a 11.4-fold variation in Mg, a 3.0-fold variation in P, and a 8.8-fold variation in K, were found among tree species. Protein varied 4.0-fold and phenols 21-fold. Interspecific differences in chemistry, summarized by Principal Components Analysis (Fig. 3) showed that N, P, K, Mg, Ca, protein, phenol and tannins loaded positively, but C and Lamina Fracture (a measure of leaf toughness) loaded negatively in PC1 (accounting for 69.8% of the variance). Only Mg, Ca and protein had positive loadings in PC2 (14.9% of the variance). In sum, there was ample evidence for tree species-based differences in litter depth, chemistry and distribution, and for deeper, more homogenous litter close to the trunk.

Testing the tree specialization hypothesis

On average, only 41% of arthropod species (52.7% of oribatids, 24.2% of gamasids, and 46.2% of ants) were common enough to be included in the specificity (IndVal) analysis. From these, only 12.5–33.33% of our focal taxa specialized on a given tree species (Table 2). Oribatids had the most specialists (5 of 15), gamasids the second most (3 of 16), and ants the least (4 of 32). Tree species, which hosted the most specialists, were *C. alliodora* (with one ant,

Table 2 Quantitative results of the litter arthropod sampling. Arthropod abundance (n/Ind) and diversity (S/Ind ; Fisher's Alpha) varied across tree taxa

Tree code	n/Ind	S/Ind	Fisher's Alpha	IndVal (specificity)	SAC	SAC_SD
Ants						
ALco	55.3	11.3	10.2	–	Yes	Yes
ANex	62.0	12.5	10.8	<i>Pheidole mendicula</i> - <i>P. rugiceps</i>	Yes	Yes
ASgr	48.4	12.0	11.8	–	Yes	Yes
CEob	45.1	12.0	11.3	–	Yes	Yes
COal	47.0	11.9	11.9	<i>Pheidole</i> sp. 2	Yes	Yes
DEar	72.0	15.1	12.3	<i>Solenopsis</i> sp. 2	No	No
PRte	49.6	11.7	10.3	–	Yes	Yes
TAve	66.0	12.6	11.3	–	No	Yes
TRmi	53.1	12.4	12.7	–	No	No
VImu	42.1	10.1	10.5	–	No	No
Gamasids						
ALco	8.7	4.2	12.2	Gamasid sp. 21	Yes	Yes
ANex	5.5	2.9	4.7	Gamasid sp. 14	No	No
ASgr	7.2	3.0	9.0	–	Yes	Yes
CEob	7.8	4.4	14.5	–	No	No
COal	7.9	4.6	14.0	Gamasid sp. 19	Yes	Yes
DEar	7.6	3.2	7.4	–	Yes	Yes
PRte	7.3	3.9	13.2	–	Yes	Yes
TAve	6.3	3.3	8.0	–	No	No
TRmi	7.4	3.0	8.6	–	No	No
VImu	4.9	3.3	8.0	–	No	No
Oribatids						
ALco	42.3	5.9	4.4	Oribatid. sp. 7	Yes	Yes
ANex	48.5	6.8	2.9	–	Yes	Yes
ASgr	38.6	6.4	4.8	–	Yes	Yes
CEob	46.2	6.9	5.4	Oribatid sp. 167	Yes	Yes
COal	36.8	5.7	5.4	Oribatid sp. 164	Yes	Yes
DEar	107.0	4.7	2.3	Oribatid sp. 147	No	Yes
PRte	52.7	5.1	3.2	–	Yes	Yes
TAve	36.8	5.7	3.5	–	Yes	Yes
TRmi	49.7	4.9	4.0	–	Yes	Yes
VImu	65.6	5.8	2.8	Oribatid sp. 150	Yes	Yes

Results of IndVal (specificity) analysis are reported, showing arthropod species characteristic for a given tree species. We report if species accumulation curves (SAC) of arthropod under tree species have reached the plateau and if the standard deviation (SAC_SD) has decreased, with sampling

one gamasid, and one oribatid species) and *A. excelsum* (with two ant and one mite species) hosted the most specialists. We could not detect arthropod specialists underneath the canopy of *Astronium graveolens*, *Protium tenuifolium*, *Tachigalia versicolor*, and *Trema micrantha* (Table 2).

Overall differences among species in terms of the collective arthropod assemblages, as summarized by non-metric multidimensional scaling, were small (Fig. 4). Stress levels were high for ant (NMDS, Stress = 0.382, $R^2 = 0.90$), gamasid (NMDS, Stress = 0.24, $R^2 = 0.94$), and oribatid (NMDS, Stress = 0.23, $R^2 = 0.946$) assemblages underneath tree canopies. However, ANOSIM analyses revealed that gamasid assemblages ($R = 0.1273$, $P < 0.001$) but not oribatid ($R = 0.2937$, $P < 0.0893$) or ant ($R = 0.0269$,

$P < 0.1476$) assemblages, differed significantly between several tree species pairs: *A. excelsum*–*C. obtusifolia*, *A. excelsum*–*C. alliodora*, *A. excelsum*–*D. arboreus*, *V. multiflora*–*C. obtusifolia*, and *V. multiflora*–*Trema micrantha* (Table 3).

Even though litter underneath tree canopies is more homogeneous (see previous results), arthropod assemblages underneath tree canopies were not less diverse or abundant in 1 m plots than in 30 m plots (Table 4). In fact, gamasid assemblages, contrary to expectations, were more abundant and diverse next to *T. micrantha* and *V. multiflora* individuals than in plots 30 m away [(Gamasid abundance), ANCOVA, tree treatment, $F = 7.013$, $P = 0.008$, tree \times distance treatment $F = 5.219$, $P = 0.023$; (Gamasid diversity), ANCOVA, tree treatment, $F = 6.2537$,

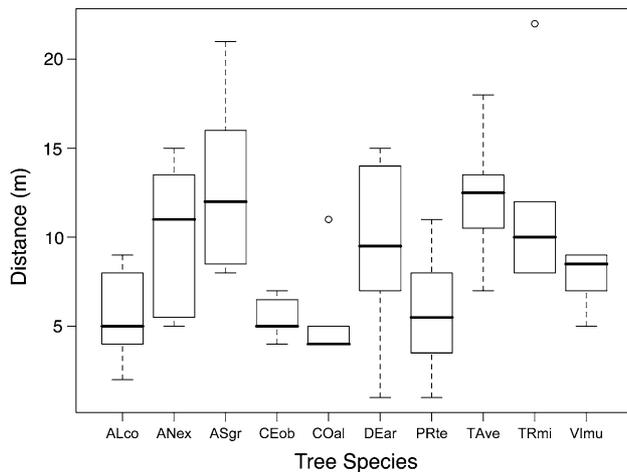


Fig. 2 Boxplots of the litter fall footprint for 10 Neotropical tree species. Trees species differed in the distance their litter reaches from the parent trunk, maintaining heterogeneity in the litter substrate. Tree species labels are explained in Table 1

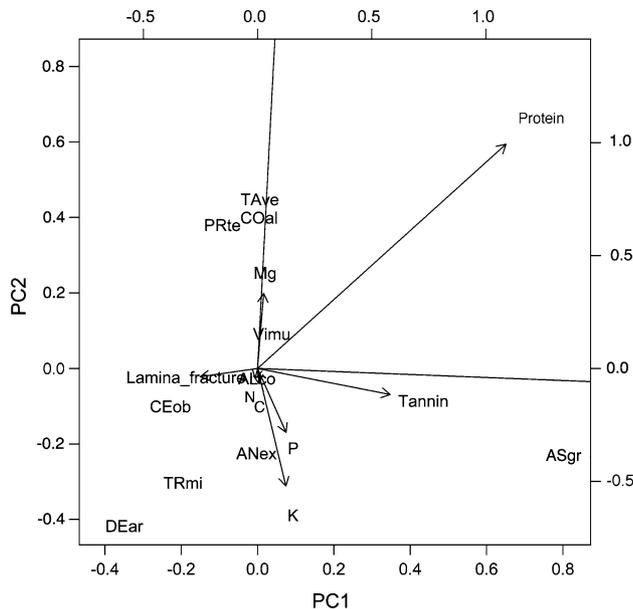


Fig. 3 PC analysis of litter chemistry from ten tree species showed that litter among trees varied in chemical composition. Tree species labels are explained in Table 1. Only C and Lamina Fracture loaded negatively in *PC1*, which explained most of the variance (69.8% of the variance). Mg, Ca and Protein had positive loadings in *PC2* (14.9% of the variance). Vectors represent loadings of scaled (5×) chemical variables in our study

$P = 0.012$, tree \times distance treatment, $F = 3.120$, $P = 0.078$] (Table 4).

Testing the abundance–extinction hypothesis

We found no evidence that either arthropod abundance or litter depth are correlated with arthropod diversity (Fisher's Alpha) underneath tree species (Gamasids, S vs N , $R^2 = 0.20$;

S vs litter depth, $R^2 = 0.0025$. Oribatids, S vs N , $R^2 = 0.01$, S vs litter depth, $R^2 = 0.0209$. Ants, S vs N , $R^2 = 0.0241$; S vs litter depth, $R^2 = 0.0119$).

Discussion

Tropical forests' canopies sustain many of the most biodiverse groups of arthropods in the world such as beetles and butterflies (Erwin 1982) but little is known about their role in producing and maintaining soil arthropod biodiversity. In fact, trees are natural candidates to produce and maintain high heterogeneity levels in tropical forest floors, and previous research has found positive responses of litter arthropods to litter chemistry and structural variability in agroecosystems (Fromm et al. 1993), grasslands, (St. John et al. 2006), and tropical forests (Burghouts et al. 1992; Medianero et al. 2007). Here, we tested the tree specialization hypothesis, which assumes that litter habitat characteristics differ and that species specialize on different parts of this habitat. We characterized and found significant differences in four attributes of known importance to litter arthropods in 10 tropical tree species (litter depth, litter fall footprint, litter identity heterogeneity, and litter chemistry). Litter was consistently deeper and more homogeneous in areas closer to the tree trunks than in random plots located 30 m away. However, despite considerable tree species-based heterogeneity across a tropical forest floor, only a small fraction of ant, gamasid, and oribatid species, three of the most diverse and ecologically dominant taxa in the litter, showed signs of specialization to tree species resources at local (<1 m²) scales. Our results suggest that differences in soil taxa diversity at larger spatial scales (e.g., temperate vs tropical forests) may not be correlated with tree diversity in these forests.

Reasons exist, however, to doubt that tree species generate diversity in BFWs. Litter arthropods are assumed to be generalists, because they do not interact directly with living plants, but harvest nutrients from dead plant material and the microbes decomposing the litter (Seastedt 1984; Moore et al. 1988). The microbial turf is likely a more homogeneous and nutrient-rich substrate than leaf litter (Swift 1976; Illig et al. 2005), and it is the substrate upon which most arthropods of tropical BFWs, being fungivores (Fittkau and Klinge 1973), feed. Furthermore, species-specific leaf fall (Williams et al. 2008) and steady rates of microbial decomposition through the year transform leaf litter into a patchy and ephemeral resource (Powers et al. 2004). As a consequence, in order to persist through the year, tropical litter arthropods must be able to grow and reproduce across a wide spectrum of litter depth and quality. We hypothesize that it is this interaction between litter decomposition and microbial diversity, and not tree identity, which may better

Fig. 4 NMDS plots for **a** oribatids, **b** gamasids, and **c** ant assemblages under tree individuals. Numbers in the graph correspond to tree species in Table 1. Dissimilarity among samples, expressed by Stress levels, were high for all arthropod assemblages underneath tree canopies (Ants Stress = 0.382, $R^2 = 0.90$; Gamasids Stress = 0.24, $R^2 = 0.94$; Oribatid Stress = 0.23, $R^2 = 0.946$)

predict gradients of soil biodiversity in forest floors worldwide.

Current theory states that species in lower trophic levels of a food web harvest resources in the proportion they occur in nature and thus may be more patchily distributed than predators (the fine-grain coarse-grain hypothesis; MacArthur and Levins 1964; Anderson 1975; Usher 1976). Contrary to theory, our analysis of arthropod assemblages revealed small, but higher, levels of patchiness for predatory arthropods. For example, in our study, the few tree species pairs with differences in arthropod species composition supported different predatory gamasid mites. These results suggest that litter arthropods' trophic level may serve as a mechanism to explain gradients of soil biodiversity and distribution across tropical forest floors.

Interestingly, arthropod abundance and diversity were not correlated with litter depth (irrespective of its chemical composition) in our study plots. Litter and its depth are of great importance to litter-dwelling arthropods (Kaspari and Yanoviak 2008). Litter accumulation creates habitat space required by litter arthropods. Litter also provides food and energy resources to microbes and saprophagous arthropods, indirectly affecting all members of BFWs. Arthropods in leaf litter may be forced to constantly migrate from a shallow, recalcitrant patch to a deeper, nutrient-rich patch, irrespective of the tree species that produces it. However, in our survey, arthropod abundance and diversity did not correlate with the litter depth profiles of our tree species. For example, *Dendropanax arboreus*, the tree species with the greatest ant abundance recorded ($n = 72$ ants/individual) and highest expected ant diversity (Fisher's Alpha = 12.3), ranked 9th in average litter depth (1.18 cm).

It is remarkable that two tree species with similar patterns of litter depth, litter fall footprint, and chemical characteristics, *Anacardium excelsum* and *Protium tenuifolium*, exhibited contrasting patterns of arthropod specificity. Two ants (*Pheidole mendicula* and *P. rugiceps*) and one gamasid mite (Gamasid sp. 14) preferred *A. excelsum* trees, but no ant or mite species was consistently found under *P. tenuifolium*. These patterns suggest that tree species may vary considerably in their ability to modify litter. Possible explanations for this pattern include the way tree species differ in leaf size and palatability, the production of branches versus leaves and other phenological differences

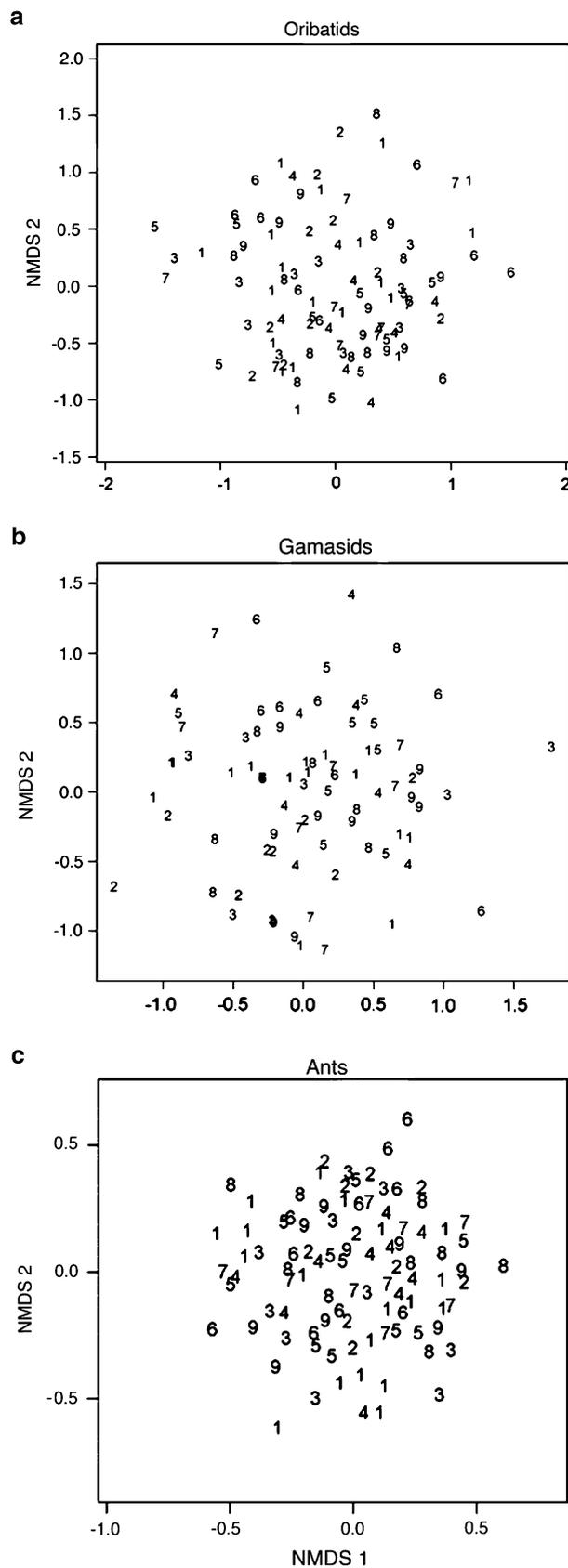


Table 3 ANOSIM results for differences in arthropod assemblage composition among tree species were significant only for gamasid mites

Pairwise comparisons of assemblages between tree species are reported
 Values in bold indicates significance at $P < 0.05$, after Bonferroni correction

	ALco	ANex	ASgr	CEob	COal	DEar	PRte	TAve	TRmi	VImu
ALco										
ANex	1									
ASgr	1	1								
CEob	1	0.018	0.405							
COal	1	0.027	1	1						
DEar	1	0	0.306	1	1					
PRte	1	1	1	1	1	1				
TAve	1	0.882	1	1	1	0.1035	1			
TRmi	1	1	1	1	0.8685	0.126	1	1		
VImu	0.675	0.054	1	0.018	1	0.099	1	1	0.018	

Table 4 Testing the tree specialization hypothesis. ANCOVAs results show that diversity and abundance of arthropods in the litter did not increase (except for gamasids) with distance from the parent trunk

	df	SS	F	P
Gamasid abundance				
Tree	1	120.9	7.013	0.008
Distance	1	1.1	0.061	0.804
Tree × distance	1	89.9	5.219	0.023
Residuals	274	4,721.5		
Gamasid diversity				
Tree	1	15.8	6.253	0.013
Distance	1	1.84	0.726	0.395
Tree × distance	1	7.89	3.120	0.078
Residuals	274	692.45		
Oribatid abundance				
Tree	1	250	0.1091	0.742
Distance	1	37	0.0163	0.899
Tree × distance	1	488	0.2125	0.645
Residuals	274	628,846		
Oribatid diversity				
Tree	1	16.7	0.296	0.587
Distance	1	0.003334	<0.001	0.994
Tree × distance	1	42.7	0.756	0.385
Residuals	274	15,456.1		
Ant abundance				
Tree	1	887	1.973	0.161
Distance	1	759	1.687	0.195
Tree × distance	1	210	0.466	0.495
Residuals	274	123,234		
Ant abundance				
Tree	1	17.36	1.879	0.172
Distance	1	10.94	1.184	0.278
Tree × distance	1	2.54	0.276	0.600
Residuals	274	2,530.81		

The relationship kept constant across tree species
 Significance values at $P < 0.05$ are in bold

such as fruit and seed size. Thus, although our target tree species were chosen to represent the wide range of phenologies and nutrient content that occurs in tropical trees, our results are specific to the tree species analyzed, and further analysis of additional tree species across this and other forests is further required to test the generality of our results.

Our conclusions are limited, in part, by the design of our study. For example, current progress in studies of herbivore host specificity are achieved by exploring how and why arthropods specialized not to tree species but to tree genera or even families (Basset 1992; Novotny and Basset 2005). Our sampling, however, did not include congenetics. Second, as rare arthropod species in the litter are usually the rule rather than the exception, our tree specialization analyses were restricted to a fraction of our surveyed arthropods, such that we were unable to determine the impact that rare species might have in our results. Finally, our measures of litter depth and heterogeneity in leaf composition are coarse and may not be sufficient to describe the many ways litter can be heterogeneous to litter arthropods. Future studies may benefit from considering finer categories in resource abundance and arthropod use, such as flowers, fruits, seeds, and branches.

Erwin’s original calculation for the total biodiversity on the earth is usually challenged by careful examination of variation encountered in one or more of his four original variables (André et al. 1994, 2002). Namely, estimators of the world’s biodiversity extrapolate (1) the number of insects specialized to a given tree species; (2) the number of tree species in an area; (3) the percentage of the total number of arthropod species that are beetles; and (4) how much more species-rich is the canopy than the litter (Erwin 1982). The number of species present on the planet is then linked to an extraordinary number of beetles that evolved as specialists to the canopy (May 1988). Current work is aimed to describe and refine the extent of the variability encountered across the planet within these variables (Longino and Nadkarni 1990; Brühl et al. 1998; Stork and

Grimbacher 2006). Our results add to this debate as we provide for the first time information on the degree of specificity to tree species that important litter faunal groups, such as mites and ants, can reach in a different substrate (e.g., leaf litter). Future studies in the area should benefit from careful examination to links between soil arthropods and microbial diversity.

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