UNIVERSITY OF OKLAHOMA

GRADUATE COLLEGE

TREES AS ECOLOGICAL TEMPLATES FOR TROPICAL LITTER ARTHROPOD COMMUNITIES

A DISSERTATION

SUBMITTED TO THE GRADUATE FACULTY

in partial fulfillment of the requirements for the

Degree of

DOCTOR OF PHILOSOPHY

By

DAVID ANDRES DONOSO VARGAS
Norman, Oklahoma
2012

TREES AS ECOLOGICAL TEMPLATES FOR TROPICAL LITTER ARTHROPOD COMMUNITIES

A DISSERTATION APROVED FOR THE
DEPARTMENT OF ZOOLOGY

BY

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To my dad, Diego Francisco Donoso Chavez,

And to my mom, Giomar Vargas Flores,

who always support me.

ACKNOWLEDGEMENTS

I thank my dissertation committee for continuous support during my program. Drs. Michael Kaspari, Richard Broughton, Yiqi Luo, Laurie Vitt and May Yuan oversaw and improved this work in many ways. Many people loaned specimens, provided taxonomic identifications, and authored all the manuscripts upon which this work is based. I thank them all. I want to give special thanks to the persons of Bill Matthews, Mike Kaspari, Jon Shik and Alex Wild who were fundamental in me coming and staying in the program. And, I want to thank to the ants for providing inspiration and constant reminder of what science is all about.

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In Chapter 3, I reviewed the systematic status of the Neotropical ant genus *Tatuidris*. It is currently submitted to *Zootaxa*.

In Chapter 4, I conducted an experiment to explore the consecuences of high ant abundance in brown food webs. It is currently submitted to *Journal of Animal Ecology*.

In Chapter 5, I explored mechanisms of ant species co-existence using trait- and phylogenetic-based test of community composition. It is currently formatted for submission to *Ecography*.

CHAPTER 1: 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 tropical 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 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, Bargett, Yeates et al. 2005, 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, Novotny et al. 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 the recycling of nutrients and releasing the energy locked in all plant tissues (Coleman et al. 2004, Bardgett 2005, Bardgett, Usher et al. 2005). 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 co-evolve (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, Yanoviak and Kaspari 2000, André et al. 2002, 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 (e.g. < 1 km^2), 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, 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, Sheu 2005, St. John et al. 2006).

Second, the TSH requires 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, Sheu 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 (Armbrecht 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, Sheu 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 (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 10 tree species in a Panama rainforest at local scales. First, we investigated the extent of the variability in four tree traits (litter depth, litter chemistry, leaf species heterogeneity and litter fall footprint), among 10 tree species of known importance to litter arthropods. We then tested the TSH by assaying the extent of specialization of these arthropod groups to 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 microbivore microarthropods, 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 (LN 09º 06', LW 079º 50'). BCI is a 420 km^2 lowland seasonal moist forest (2400 mm average annual rainfall and 18 ºC 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 ten 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, Armbrecht 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 tree species were gathered from Dominy et al. (2003). Leaf species heterogeneity (# leaf species contained in 0.25 m^2) was measured 1 and 30 m away from each tree individual in a random direction in June 2003. A 0.25 m^2 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 vs. 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 R v.2.8.1 (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 ten target tree species (Table 1). Two litter samples were taken from two 0.25 m^2 quadrats located 1 m away at opposite sides of the trunk. 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. 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 an efficient, passive method, for sampling litter arthropods (Donoso et al. 2009). Oribatids, gamasids, and ants were sorted to morphospecies. We identified ants using standard taxonomic keys. Dr. Heinrich Schatz identified mites to the species–morphospecies level. All specimens were deposited in the collection of MK 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) vs. far (30m) assemblages (see below), we selected randomly one of the two 1 m quadrats. 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 an 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 5000 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 30m away quadrats). For gamasids and 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 8 individuals (for mites) and 8 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 the statistical software R 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 was depicted by the relative distances separating them in a two-dimensional space (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 similarities in arthropod assemblage composition equal between–tree similarities. ANOSIM provides a test statistic R, with values close to 1 meaning significant 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, version 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 30m away. For this analysis we selected randomly one of the two near (1m) arthropod samples before comparison with 30m 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 228 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 1 m quadrats, 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 (Figure 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 spp) were found under all ten 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 the 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 251 (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), and expected richness (Fisher's Alpha = 5.4) of oribatids. Gamasid abundance was highest in *Alchornea costarricense* (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 $F_{9,56} = 4.281$, $p < 0.001$) (Figure 2). Leaves of Alchornea costaricensis fell nearest to the parent trunk (5.5 m ± 2.66,), whereas leaves of Astronium graveolens fell further from the trunk (12.33 m ± 4.99). Litter depth 1m from the trunk varied 3-fold across tree species (ANOVA, F9. 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 30m away (ANCOVA, $F_{1,140}$=12.90, $p < 0.001$, tree*distance interaction, $F_{19,140} = 1.41$, $p = 0.189$). Litter heterogeneity (# leaf species contained in 0.25 m^2) was consistently higher by almost two-fold in samples 30m 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*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 Nitrogen concentration, a 11.4–fold variation in Magnesium, a 3.0–fold variation in Phosphorus, and a 8.8–fold variation in Potassium, were found among tree species. Protein varied 4.0-13 fold and phenols 21-fold. Interspecific differences in chemistry, summarized by Principal Components Analysis (Figure 3) showed that Nitrogen, Phosphorus, Potassium, Magnesium, Calcium, Protein, Phenol and Tannins loaded positively, but Carbom and Lamina Fracture (a measure of leaf toughness) loaded negatively in PC1 (accounting for 69.8% of the variance). Only Magnessium, Calcium 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 *Cordia alliodora* (with one ant, one gamasid, and one oribatid species) and *Anacardium 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 tennuifolium*, *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 (Figure 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 = 0.02699, $p < 0.1476$) assemblages, differed significantly between several tree species pairs: *A. excelsum–C. obtusifolia*, *A. excelsum–C. alliodora*, *A. excelsum–D. arboreus*, *V. multiflora–C. obtusifolia*, *V. multiflora–Trema micrantra*, and *V. multiflora–D. arboreus* (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 1m plots than in 30m 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 30m away ([Gamasid Abundance], ANCOVA, tree treatment, F = 7.0135, $p = 0.008$, tree*distance treatment F = 5.2191, $p = 0.023$; [Gamasid Diversity], ANCOVA, tree treatment, F = 6.2537, $p = 0.012$, tree*distance treatment, F = 3.1209, $p = 0.07841$) (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,

richness vs. abundance, $R^2 = 0.200$; richness vs. litter depth, $R^2 = 0.003$. Oribatids, richness vs. abundance, $R^2 = 0.010$, richness vs. litter depth, $R^2 = 0.021$. Ants, richness vs. abundance, $R^2 = 0.024$; richness vs. litter depth, $R^2 = 0.012$).

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 these, local, 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 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 tennuifolium*, 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. tennuifolium*. 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 biomass production (leaf, seed and fruit size) and palatability, and other phenological differences in the appearance of leaves, fruits and seeds. 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 be achieved by exploring how and why arthropods specialized not to tree species, but tree genera or even families (Basset 1992, Novotny and Basset 2005). Our sampling, however, did not include congenerics. Second, as rare 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 earth is usually challenged by careful examination of variation encountered in one or more of his four original variables (Andre et al. 1994, 2002). Namely, estimators of the world's biodiversity 388 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.

Figure Legends. Chapter 1

Figure 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, 10 oribatid and 6 gamasid 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).

Figure 2. Boxplots of the *litter fall footprint* for ten 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.

Figure 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 (5X) chemical variables in our study.

Figure 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).

Figure 1. Chapter 1

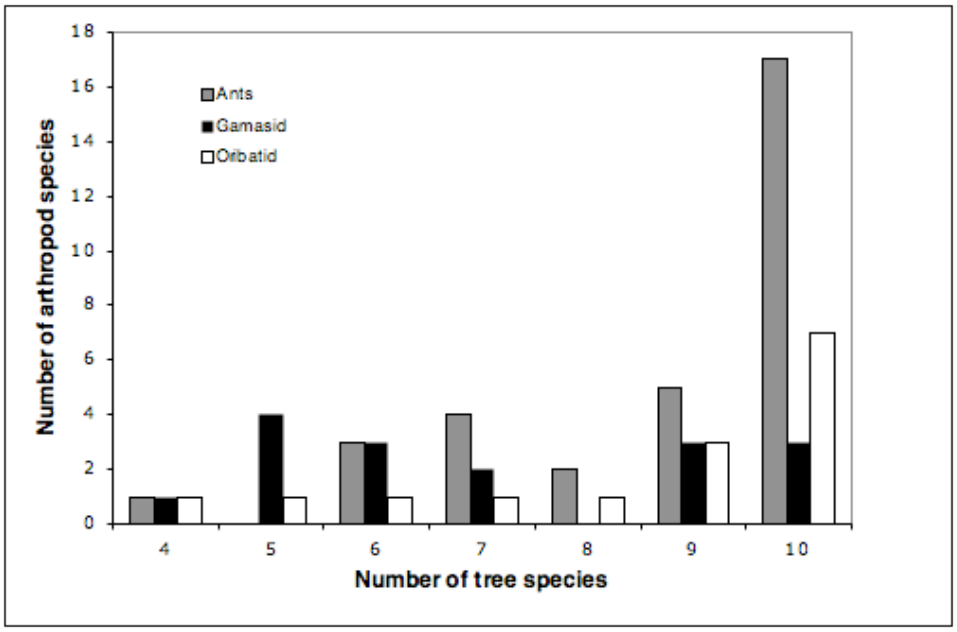

Figure 2. Chapter 1

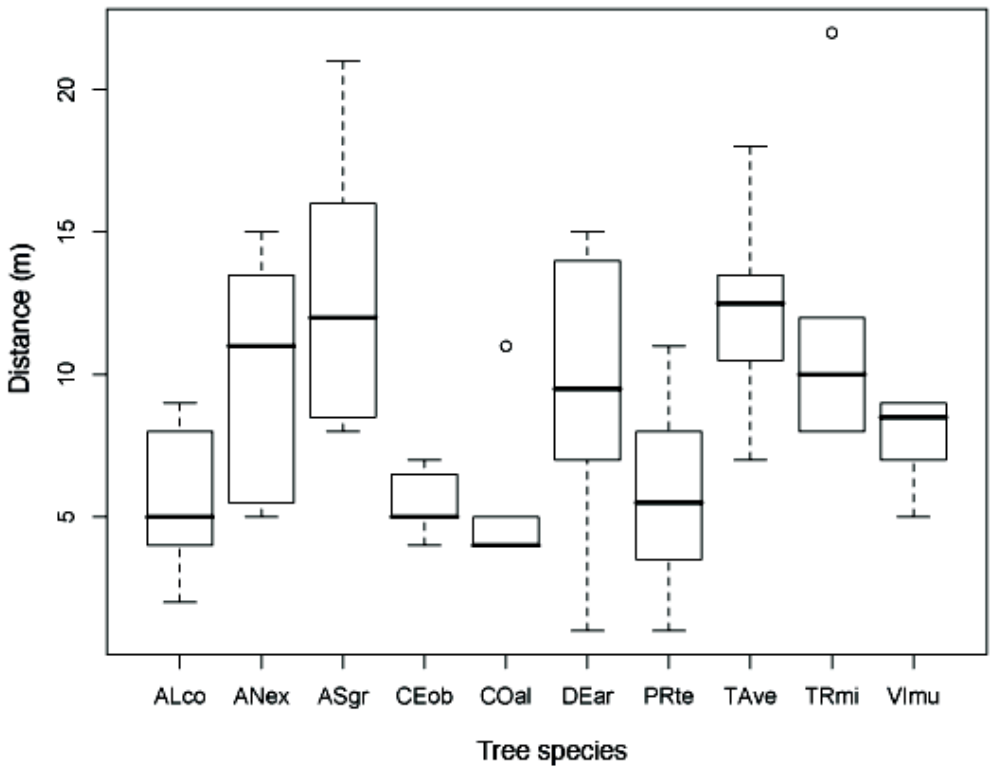

Figure 3. Chapter 1

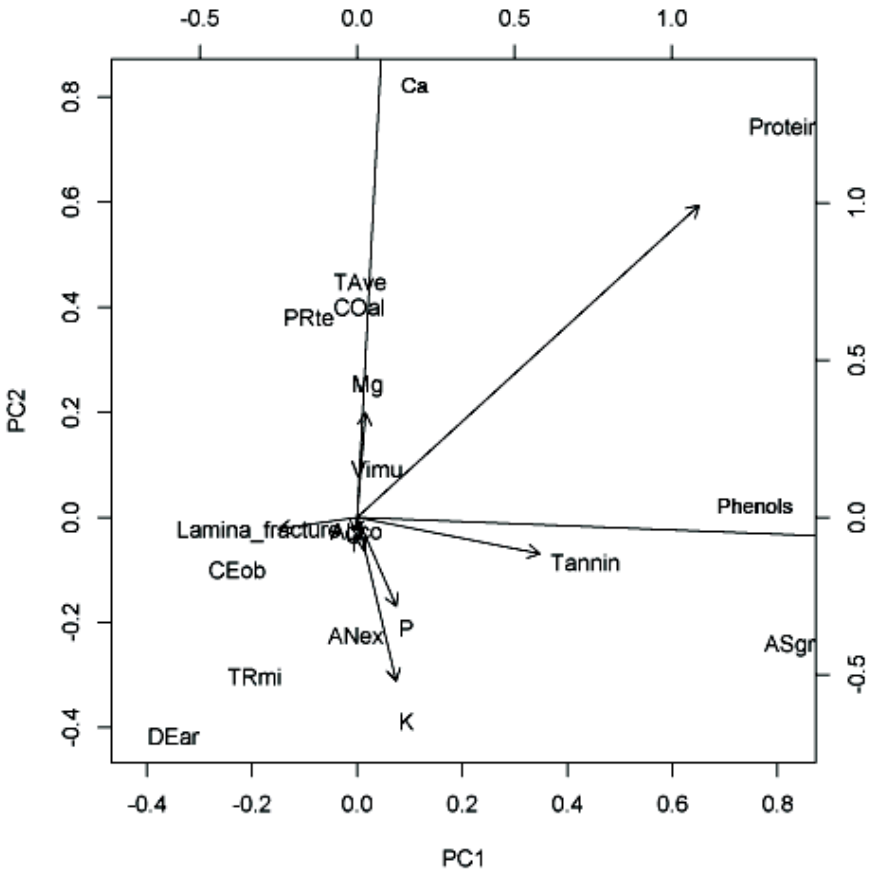

Figure 4. Chapter 1

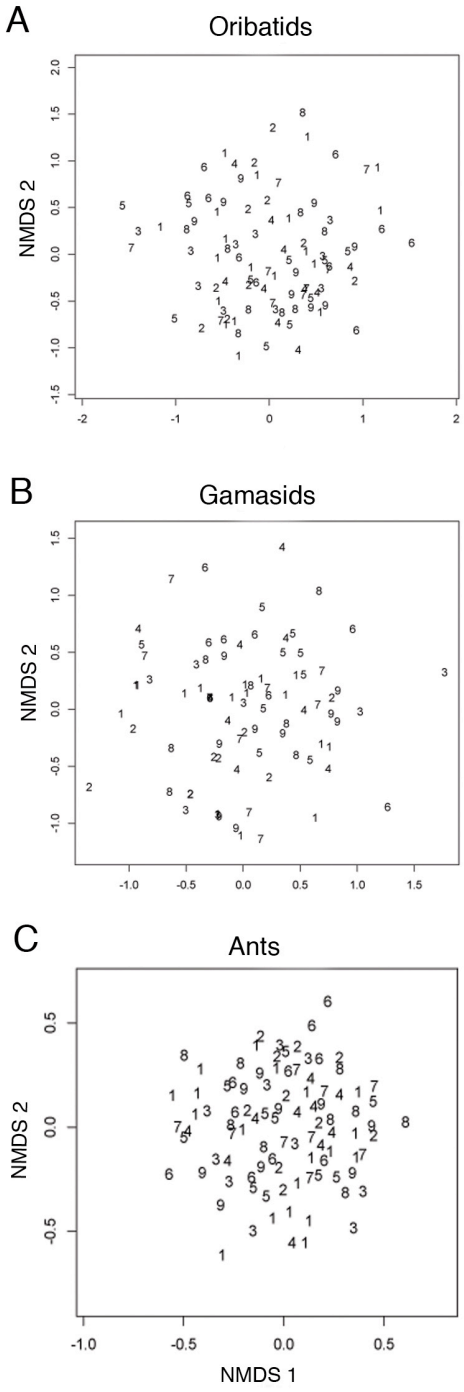

Table Legends. Chapter 1

Table 1. Characteristics of ten Neotropical tree species sampled in this study within the 50 ha CTFS plot. Tree species were assigned to one of fives chemical syndromes with possible influence on arthropods. Number of tree individuals sampled and litter depth found underneath their canopies is provided for each species.

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

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.

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

Table 1. Chapter 1

#	Code	Genus/Species	Syndrome	# Ind	Litter Depth (cm)
1	ALco	*Alchornea*	+palatability	10	1.61
2	ANex	*Anacardium*	+tannin; +lignin	10	3.46
3	ASgr	*Astronium*	+tannin	9	1.39
4	CEob	*Cecropia*	+palatability	10	1.22
5	COal	*Cordia alliodora*	+calcium	10	1.25
6	DEar	*Dendropanax*	+lignin	9	1.18
7	PRte	*Protium tenuifolium*	+tannin; +lignin	9	2.04
8	TAve	*Tachigali*	+calcium	9	2.86
9	TRmi	*Trema micrantha*	+lignin	8	0.94
10	VImu	*Virola multiflora*	+tannin	9	1.8

Table 2. Chapter 1

Ants						
Tree Code	N/Ind	S/Ind	Fisher's Alpha	IndVal (specificity)	SAC	SAC_SD
ALco	55.3	11.3	10.2	-	yes	yes
ANex	62.0	12.5	10.8	*Pheidole mendicula - P. rugiceps*	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	*Pheidole* sp.2	yes	yes
DEar	72.0	15.1	12.3	*Solenopsis* 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

Table 3. Chapter 1

	ALco	ANex	ASgr	CEob	COal	DEar	PRte	TAve	TRmi
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. Chapter 1

Gamasid Abundance	Df	SS	F	*P*
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	4721.5		

Gamasid Diversity	Df	SS	F	*P*
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	Df	SS	F	*P*
tree	1	250	0.1091	0.742
distance	1	37	0.0163	0.899
tree:distance	1	488	0.2125	0.645
residuals	274	628846		

Oribatid Diversity	Df	SS	F	*P*
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	15456.1		

Ant Abundance	Df	SS	F	*P*
tree	1	887	1.973	0.161
distance	1	759	1.687	0.195
tree:distance	1	210	0.466	0.495
residuals	274	123234		

Ant Diversity	Df	SS	F	*P*
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	2530.81		

CHAPTER 2: TREES AS TEMPLATES FOR TROPHIC STRUCTURE OF TROPICAL LITTER ARTHROPOD COMMUNITIES

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Abstract

Litter arthropods in tropical forests are diverse and patchily distributed in space and time. This patchiness can be described by two general hypotheses relating plant-based effects to litter arthropod distribution. The Tree Hypothesis posits that environments maintained underneath tree canopies are different from those between canopies in ways that shape arthropod distribution. The Species Hypothesis posits that different plant species maintain distinct litter environments to which arthropod distribution respond. One, both, or neither can be true, yet little work has simultaneously tested these possibilities or their mechanisms. The Ecosystem Size Hypothesis (ESH) provides a mechanism for tree or species effects. It states that greater litter volumes increase food chain length by increasing arthropod abundance in lower trophic levels. In a Panama rainforest we sampled litter arthropods in quadrats located near (1m) and far away (30m) from the parent trunk (to test the Tree Hypothesis) of 93 tree individuals 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 in litter profiles, we then resample 25 trees (i.e., five individuals from each of five species) in the late wet season, when litter is most shallow. We did not find strong support for the Tree or Species Hypotheses; with few exceptions, trees and species did not sustain different arthropod taxa abundance. Supporting the ESH, accumulated litter either due to trees or species effects sustained higher predator abundance and higher predator to prey ratios, a measure of food chain length. These results escalated in late wet season when patches of deep litter are rarer. Our results suggest that plants through tree effects account for BFW structure; but weak species effects may limit the maintenance of plant-based clues

necessary for BFW diversification. We extend the ESH to litter environments and suggest a framework to understand plant-based bottom-up forces in structuring litter communities.

Keywords. Tree Hypothesis, Species Hypothesis, Ecosystem Size Hypothesis, brown food web, tropical forest, litter arthropods, predator to prey ratios.

Introduction

Explaining the high patchiness in abundance and trophic structure 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 by providing nutrients and habitat conditions required for litter arthropod survival (Finzi *et al.* 1998; Wardle 2005; Moore *et al.* 2004; Bardgett and Wardle 2010). The Tree Hypothesis (TH), proposed here, posits that litter directly below tree canopies differs (e.g., in volume, structure or chemistry) from that farther away, in ways that may account for patchiness in BFW structure. A second hypothesis, the Species Hypothesis (SH) posits that interspecific differences in litter traits may account for the patchiness in BFW structure (Erwin 1982, Bezemer *et al.* 2010) and different plant species will 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 specific arthropod fauna feeding upon microbes and other arthropod groups (De Deyn *et al.* 2004, Barton *et al.* 2010, but see Donoso *et al.* 2010).

Taking into account these two hypotheses, tropical plants effects on BFWs may be understood within a simple framework (Table 1): if both tree and species effects are present, then BFW structure may change strongly across the forest floor, reflecting tree species identity and distribution (Donoso *et al.* 2010). This scenario, built upon Erwin's (1982) work, is rooted in niche theory and predicts BFW biodiversity and structure to be highly 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 specific clues for its diversification. 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 in which species but not tree effects are found suggest that associations of BFWs to tree species are due to stronger effects of a third factor, such as soil nutrients or topography (Lessard *et al.* 2010), on plant and arthropod taxa. While links between litter arthropod and plant species abound in the literature (see Bardgett and Wardle 2010 for a review), there is, however, little consensus about the specific mechanisms behind the TH and the SH, and how trees act as templates for BFWs.

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 mechanism for the TH and the SH. It assumes that larger ecosystems sustain more individuals and species at lower trophic levels, which in turn 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 or nutrient transfers from detritivores to top predators in a food web, with ecosystem size. 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 $\leq 1m^2$) provides good representations of ecosystem size because most litter arthropod's home ranges (Post 2002a) usually spread and interact with other litter arthropods within a few squared meters; e.g., in tropical forests most ant species forage within 1m from its colony entrance (Kaspari 1996). In turn, 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 shape 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). We thus posit that if tree or species differ in average litter depth maintained underneath their canopies, then the ESH may provide a mechanism for the TH and SH via litter depth's effect on BFW's trophic structure.

Litter production varies seasonally in tropical forests (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 an 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 decomposed, leaving a thin layer of relatively homogenous and recalcitrant litter. This seasonality in litter profiles may have

implications for the relationship between plants and litter arthropod communities, proposed here as the TH and SH. Tree and species effects on BFW, via the ESH, should be strongest at the start of the rainy season, when litter depth is high and chemistry is most diverse. In turn, the ESH predicts lower predator to prey ratios later in the wet season.

We explored how litter traits such as chemistry and depth explained changes in community composition. 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 used stable isotopes ($\delta^{15}N$) 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 tree individuals and species with deeper litter. Further, we explored how arthropod communities responded to seasonality, one of the main generators of temporal variability in litter profiles within a forest. We tested the prediction that tree and species effects on BFW trophic structure decrease from the early wet season, when litter was deep and heterogeneous, to late wet season, when litter was shallow and more uniform.

Materials and Methods

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-km2 lowland seasonal moist

forest with an average annual rainfall of 2,600 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).

Focal trees and arthropod taxa

Our target 10 tree species were selected in the field to represent a gradient of chemical and structural variability encountered among BCI tree species. We chose mature trees to maximize the size 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 have reported previously (Donoso *et al.* 2010) how tree species modify four key traits of tree litter known to influence BFW structure. These traits reflect variability in resource quantity and quality provided by our focal tree species (Hansen and Coleman 1998; Hansen 2000; Kaspari and Yanoviak 2009). Briefly, these traits are defined as follow 1) *litter depth,* measured from four corners of the arthropod sampling quadrat; 2) *litter fall footprint,* measured by laying out a transect in a random direction, skewering litter every 1 m, and counting the number of collected focal leaves; 3) *litter chemistry (*% N, P, K, Mg, Ca), measured from newly fallen leaves gathered from under each target tree individual; phenolic, tannin, protein, and lamina fracture levels for tree species were gathered from literature; and, 4) *leaf species heterogeneity* (the ratio of focal vs. non-focal leaves contained in 0.25-m^2), measured 1 and 30-m away from each

tree individual in a random direction, by placing a 0.25-m^2 quadrat on the litter, and estimating the number of focal and non-focal species leaves within that quadrat.

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. 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 5 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 averaged 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. All count data was ln(X+1)-transformed, except when estimating Predator to Prey ratios, prior to analysis.

Stable isotope analyses

We characterized the trophic level of our 8 target arthropod taxa using nitrogen (N) stable isotope values ($\delta^{15}N$). 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 2005). Samples consisted of multiple specimens (n=10-100) pooled from under all individuals of each of the 10 tree species. This sampling protocol yields a conservative, representative measure of trophic position of each of the eight taxa within BFWs below each of the 10 tree species. Seven additional BFW taxa [Ptiliidae (Coleoptera), Thysanoptera, Pseudoscorpionida, Diptera larvae, Carabidae (Coleoptera), Termites (Isoptera) and Opiliones] that did not yield enough material under each tree species were included in this analysis to provide a more comprehensive view of the Barro Colorado BFW trophic structure. In this case, all available material from these seven groups was grouped under one sample. All arthropod's body parts, excluding guts, were homogenized for all taxa. However, for small-size taxa such as Oribatida, Mesostigmata, Collembola, Thysanoptera, Diptera larvae and Pseudoscorpionida, we homogenized whole bodies (including guts). Trophic position (TP) was calculated with the following formula $TP = \lambda + (\delta^{15}N_{secondary\ consumer} - \delta^{15}N_{Base}) / \Delta_N$, where $\lambda = 2$ (i.e., Ptiliids, the organism in our database with the lowest $\delta^{15}N$, is a – fungi – primary consumer); $\delta^{15}N_{Base}$ for Ptiliids is 3.876, and we assumed trophic enrichment Δ_N of

3.4‰ for each trophic level (Post 2002b, McCutchan *et al.* 2003).

All taxa were preserved in 95% ethanol prior to stable isotope analysis. Ethanol fixation is known to affect the isotopic status of the organisms, but these changes are here assumed to be minimum (Barrow *et al.* 2008). We first dried all samples at 60°C and then we encapsulated ~500 µg of each homogenate into tin capsules. Stable isotopes of nitrogen were analyzed using a CosTech Elemental Analyzer interfaced through a ConFlo III open split valve with a Thermo Finnigan Delta V isotope ratio mass spectrometer. We report N isotope values using delta notation ($\delta^{15}N$) where $\delta = ((R_{sample}/R_{standard}) - 1) \times 1000$; R = ratio of heavy to light isotope ($^{15}N/^{14}N$ for nitrogen stable isotopes) of the sample and standard. Delta values are expressed in ‰ (per mil notation). A laboratory standard of powdered Brown Headed Cow Bird feathers was measured and referenced against the international standards for N of Peedee Belemnite (PDB) and atmospheric nitrogen respectively. Based on values from the laboratory standards, we calculated N stable isotope precision as ±0.119‰ (N = 9). We used one-way ANOVAs and Tukey HSD to determine if $\delta^{15}N$ signatures within trophic position differed across consumer taxa.

Testing the Tree Hypothesis

The Tree Hypothesis assumes that litter arthropod abundance is variable among the forest floor and that tree effects, regardless of their specific identity, are greater directly underneath the trunk, than far away. It predicts that BFW structure will respond to proximity to tree trunks, but not its identity (species effects). We tested this hypothesis using the June arthropod survey (i.e., our largest dataset) as tree effects are

expected to be greatest in this period when precipitation and litter depth are high. We contrasted tree and species effects with ANCOVA. In our ANCOVA model, we use 'Distance' to the parent trunk as the continuous covariate and different tree species as levels of our treatment. To accept the Tree Hypothesis, we expected that distance (the covariate), but not tree species, to be significant. Accordingly, we interpreted significant tree species effects to provide partial support for the Species Hypothesis (see also next paragraph). We used Bonferroni corrected p values for multiple comparisons. When tree identity was significant, we used Tukey HSD to compare effects among combinations of tree species.

Testing the Species Hypothesis

The Species Hypothesis assumes that litter profiles are variable across tree species, and predicts that arthropod abundance is variable among tree species. We also tested the SH using the June arthropod survey. Similarly to the approach given to the TH, we tested for the SH using an ANCOVA approach. In this model, to test for differences in arthropod abundance across tree species, the different tree species were the levels of our treatment and we used litter depth as a covariate. We included litter depth in our model because it is an important determinant of community composition (see NMDS analysis below) and varies among the tree species in this study (Donoso *et al.* 2010). The inclusion of litter depth allows us to control for it effects, testing the secondary hypothesis that litter depth is an important trait promoting species-based differences in arthropod distribution. We used Bonferroni corrected p values for multiple comparisons. When tree identity was significant, we used Tukey HSD to

compare effects among combinations of tree species.

Then, we explored the influence of tree identity on litter arthropod community composition with a non-metric dimensional scaling (NMDS) using the "metaMDS" function in the Vegan library (Oksanen *et al.* 2005) from the R-project statistical package (R Development Core Team 2004). NMDS is an ordination technique that depicts samples in a low dimensional space, such that samples with similar taxonomic composition are closer together (van der Gucht *et al.* 2005). We used the Bray-Curtis index of dissimilarity. We performed these analyses using arthropod abundance data sorted to higher taxonomic ranks as described previously. We assessed the reliability of the ordination plot using the NMDS goodness of fit R^2 and a stress function (which ranges from 0 to 1). ANOSIM was used to test the null hypothesis that arthropod community structure did not differ among tree species. To explore the direction and strength of changes in community composition associated to our leaf chemical variables and litter depth, we fitted vectors to the ordination plot using the 'envfit' function in Vegan. envfit generates a R^2 goodness of fit and statistical significance through a permutation-based p value.

Testing the Ecosystem Size Hypothesis

The Ecosystem Size Hypothesis assumes that larger habitats maintain larger diversity and abundance of prey taxa, which sustain larger populations of predator taxa. 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. We tested this hypothesis using the June and November arthropod survey. First, we performed linear regressions of Predators, Preys and Predator to Prey ratios with litter depth. To test for the ESH as a mechanism for the Tree hypothesis, we explored the effects of distance to the parent truck on the abundance of Predator, Prey and Predator to Prey ratios using ANCOVA. In our model, the factor 'Distance' to the parent trunk is our covariate, and tree identity is the treatment variable. To test for the ESH as a mechanism for the Species Hypothesis, we explored the effects of tree identity on abundance of Predator, Prey and Predator to Prey ratios using ANCOVAs, with litter depth as a covariate. As before, because the tree species maintain different litter profiles, the inclusion of litter depth as a covariate allows us to control for the effects of litter depth from those of tree identity.

Seasonality

The ESH should predict lower predator to prey ratios at the end of the rainy season, when litter depth is lowest. We compared litter depth and predator to prey ratios in June vs. November samples with ANOVA. Additionally, we used G-tests of independence (Sokal and Rohlf 1995) to test whether frequency of individual arthropod taxa, or taxa gathered by trophic level (e.g., predators, omnivores and prey [microbivores and detritivores]) were independent of season.

Results

Focal arthropod taxa

In June, we collected in pooled 1-m away quadrats a total of 7,856 specimens from our 8 focal arthropod taxa (Table A2). 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.

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 (Figure 1). 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 2 trophic levels, primary consumers (i.e. prey) and predators. However, ANOVA and Tukey HSD analysis revealed the presence of three groups (ANOVA, $F_{7,72} = 43.51$, $p<0.001$). The lower trophic level (fungivores and detritivores) is composed by Collembola, Diplopoda, Oribatida and Isopoda. The second trophic level (Omnivores) includes only the Staphylinidae. The third trophic level (predators) is composed by Formicidae, Mesostigmata and Araneae (Figure 1). We grouped the eight arthropod taxa in Predator and Prey categories using the ANOVA-based results.

Testing the Tree Hypothesis

We did not find support for the Tree Hypothesis. Trees alone (without regard to its specific identity) influenced only marginally the arthropod abundance underneath their canopy. Abundance of Araneae (ANCOVA, Distance, $F_{1,172}=6.85$, $p=0.01$), Diplopoda (ANCOVA, Distance, $F_{1,172}=4.76$, $p=0.03$) and Formicidae (ANCOVA,

Distance, $F_{1,172}$=5.40, p=0.021) was higher in 1-m vs. 30-m away from the parent trunk, but these p values were not significant after Bonferroni corrections (Bonferroni p = 0.05/8 = 0.006). Instead, in partial support for the SH, the abundance of Collembola (ANCOVA, Tree, $F_{9,172}$=3.91, p<0.001) and Isopoda (ANCOVA, Tree, $F_{9,172}$=3.244, p<0.001) differed across combinations of tree species (Table 2). Tukey HSD comparisons revealed that abundance of Collembola was significantly lower in *Virola* and *Anacardium* trees (results not shown). Isopoda was significant lowest in *Cordia* trees (results not shown).

Testing the Species Hypothesis

Support for the Species Hypothesis was low. After Bonferroni correction, tree species identity only predicted the abundance of Collembola (ANCOVA, Tree, $F_{9,83}$=2.58, p<0.006) (Table 2). Tukey HSD comparisons showed that Collembola abundance was less abundant under *Virola* trees (see also Table A2). Instead, the covariate litter depth was a better predictor of arthropod abundance, especially for predator taxa. For example, abundance of Mesostigmatids (ANCOVA, Litter, $F_{1,82}$=7.87, p<0.006) and Staphylinidae (ANCOVA, Litter, $F_{1,81}$=10.34, p<0.002) increased in trees that maintain deeper litter underneath their canopies (Figure 2). The abundance of Araneae (ANCOVA, Litter, $F_{1,83}$=6.15, p<0.013), Formicidae (ANCOVA, Litter, $F_{1,83}$=7.55, p<0.007) and Diplopoda (ANCOVA, Litter, $F_{1,83}$=6.49 p<0.013) also increased in deep litter, but these results were not significant after Bonferroni correction (Bonferroni p = 0.05/8 = 0.006).

NMDS analysis depicted accurately the similarities in arthropod community composition across the forest floor (Linear R^2=0.89, Stress 0.14, k=3). Still, tree species did not differ in the structure of the communities they support (ANOSIM, R^2=0.02, p=0.124). From all chemical and leaf trait data, only leaf litter explained significantly variation in the ordination plot (R^2=0.10, p<0.001).

Testing the Ecosystem Size Hypothesis

The ESH predicts an increase of the relative proportion of predators in a sample, with litter depth. In June, when litter depth is highest, linear regressions showed and increase of predator taxa (R^2=0.22, P<0.001) and the predator to prey ratio (R^2=0.13, P<0.001). In November, when litter depth is shallowest and more homogeneous, both 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 (Figure 3).

ESH 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 (ANCOVA, Distance, $F_{1,172}$=5.15, p=0.024) and marginally less prey (ANCOVA, Distance, $F_{1,172}$=3.03, p=0.084). However predator to prey ratios failed to increase in deeper litter in near quadrats. No species effects were significant in this season, suggesting that all tree species maintain uniform amounts of predators in the area modified by their canopies. In November, when litter depth across the forest floor is shallowest and most

homogeneous, prey abundance increased in near quadrats (ANCOVA, Distance, $F_{1,62}$=6.89, p=0.011). Consequently predator to prey ratios, were lower in near quadrats, compared with far quadrats (ANCOVA, Distance, $F_{1,62}$=6.09, p=0.016). In partial support for the SH (see below), species effects were also significant in November. Tree species explained the abundance of predators (ANCOVA, Tree spp., $F_{4,62}$=4.20, p<0.005) and predator to prey ratios (ANCOVA, Tree spp., $F_{4,62}$=2.87, p=0.03). Tukey HSD revealed that *Anacardium* trees, which supported the most predators and the higher predator to prey ratios, drove these interspecific comparisons (results not shown).

ESH and Species Hypothesis.

In June, tree identity did not account for the abundance of predators, preys and predator to prey ratios. However, in support for the ESH, litter depth correlated significantly with predator abundance (ANCOVA, Litter, $F_{1,84}$=28.98, p<0.001) and consequently with predator to prey ratios (ANCOVA, Litter, $F_{1,84}$=10.18, p<0.002) (Table 3). A similar pattern emerged by the end of the rainy season. In November, litter depth but not tree identity accounted for the abundance of predators across tree species (ANCOVA, Litter, $F_{1,27}$=7.41, p<0.011) and prey (ANCOVA, Litter, $F_{1,27}$=4.37, p<0.046) abundance, but not predator to prey ratios (Table 3). As before, Tukey HSD revealed that *Anacardium* trees, which supported the deepest litter, the most predators and most prey, drove these interspecific comparisons.

Seasonality

Both litter depth and predator to prey ratios were twice as high in June than in November (Litter Depth, ANOVA $_{1, 126}$, F= 25.53, p<0.001; Predator to Prey, ANOVA $_{1, 126}$, F= 29.03, p<0.001, Figure 4). G-tests of independence used to test whether frequencies of individual arthropod taxa, by separate, or that of predator, prey and predator to prey ratios, varied with seasonality were all significant (Table 4). In general, these results were driven by an increase in the global and relative proportion of Collembola (increase 219%) in November, when litter depth but not water availability was lowest (Figure 5).

Discussion

There is growing evidence (Barton *et al.* 2010, Bardgett and Wardle 2010) that plants modify arthropod distribution 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. Tree trunks can modify BFW structure is they maintain under their canopies a different environment. Plant species can further modify BFW structure if they provide specialized environments. We tested specific predictions of litter effects on BFW structure across three natural gradients (tree, species and time) 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.

Erwin (1982) and others have suggested a high degree of specialization by canopy arthropods on tree species. But we failed to find this pattern in tropical BFWs, home to an important percentage of the world biodiversity (Coleman 2008). Trees influenced BFW taxa, but their effects were mostly independent of tree identity. For example, individual tree species did not support different target arthropod groups. Exceptions to this pattern were found mostly 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 m2 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 difficulty 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 forest 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 (Bardgett 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 Staphylinids 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 (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). These 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 ecosystem size.

A missing link in our study is the response that microbial, fungal and bacterial, communities may have to litter of different tree species and seasonality. 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 developed 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, 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 transfer of biomass from lower trophic levels to higher ones —that is, predators limiting the size of prey population (Milton and Kaspari 2007); or 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 that tree-based and season-based changes in litter depth, but not chemistry, are of importance to predator taxa in this seasonal tropical forest (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).

Figure Legends. Chapter 2

Figure 1. Boxplot with trophic level of common litter arthropod taxa for Barro Colorado Island. Arthropod groups initials are as follow “Ptil” Ptiliidae, ‘Term’ Isoptera, “Di-la” Diptera larvae, “Orib” Oribatida, “Dipl” Diplopoda, “Coll” Collembola, “Isop” Isopoda, “Cara” Carabidae, “Thys” Thysanoptera, “Stap” Staphylinidae, “Opil” Opiliones, “Form” Formicidae, “Aran” Araneae, “Meso” Mesostigmata and “Pseu” Pseudoscorpionida. Arthropod groups were ordered according to increasing trophic position values. Letters above the bars follow ANOVA and Tukey HSD comparisons results. Boxplots show the medians, inter-quartile ranges, and minimum and maximum values, with values beyond the 95% CI indicated by open circles.

Figure 2. Test for the Species Hypothesis. Linear regressions of Litter Depth against Formicidae, Staphylinid and Mesostigmatid abundance [in ln(X+1) scale], following ANCOVA results. Litter depth explained significantly the abundance of Formicidae and Staphylinids.

Figure 3. Linear regressions of Litter Depth against predator, prey and predator abundance [in ln(X+1) scale] and prey ratios in June and November surveys.

Figure 4. Effects of seasonal variability in litter depth on predator to prey ratios. Boxplot of Predator to Prey ratios and Litter Depth in different months. Both Predator to Prey ratios and Litter Depth were higher in June than in November, at the start of the

rainy season. ANOVA differences were both significant. Boxplots show the medians, interquartile ranges, and minimum and maximum values, with values beyond the 95% CI indicated by open circles.

Figure 5. Mean abundance, per sample, of different arthropod groups in June and November. G-Test comparisons of frequencies were all significant. Notice the increase of Collembola abundance in November. Arthropod groups initials are as follow: “Stap” Staphylinidae, “Aran” Araneae, “Dipl” Diplopoda, “Isop” Isopoda, “Meso” Mesostigmata, “Form” Formicidae “Orib” Oribatida and “Coll” Collembola.

Figure 1. Chapter 2

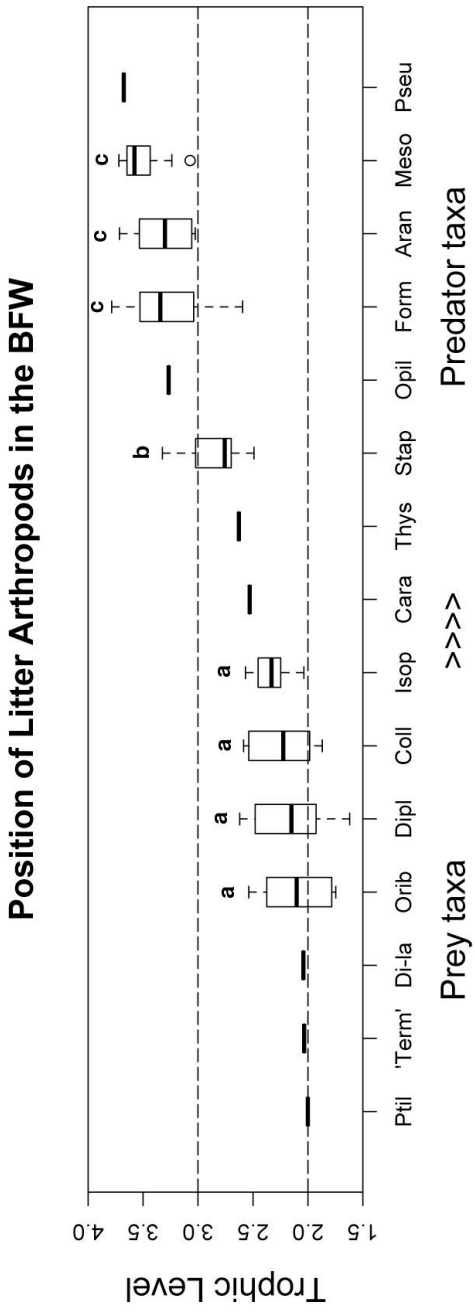

Figure 2. Chapter 2

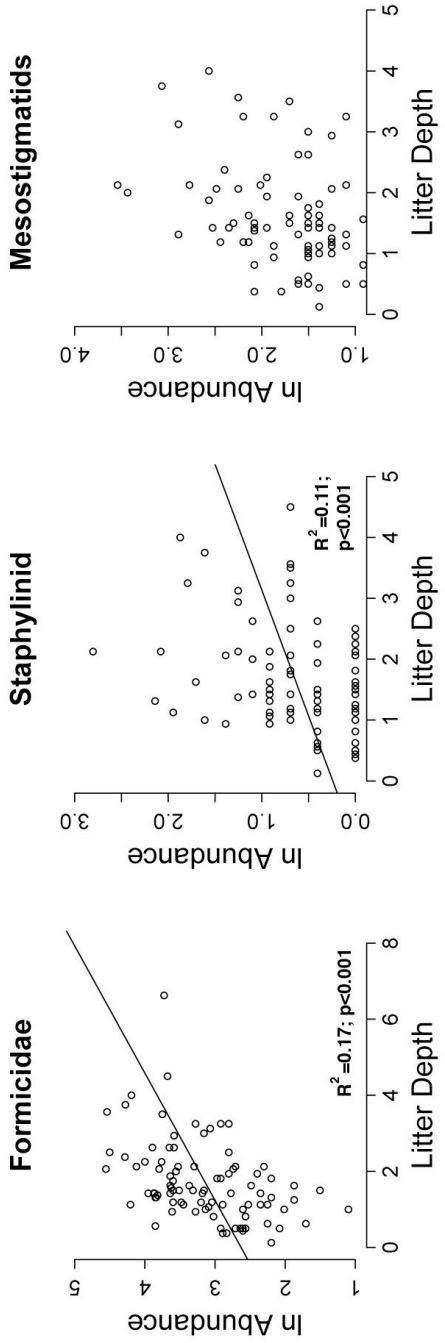

Figure 3. Chapter 2

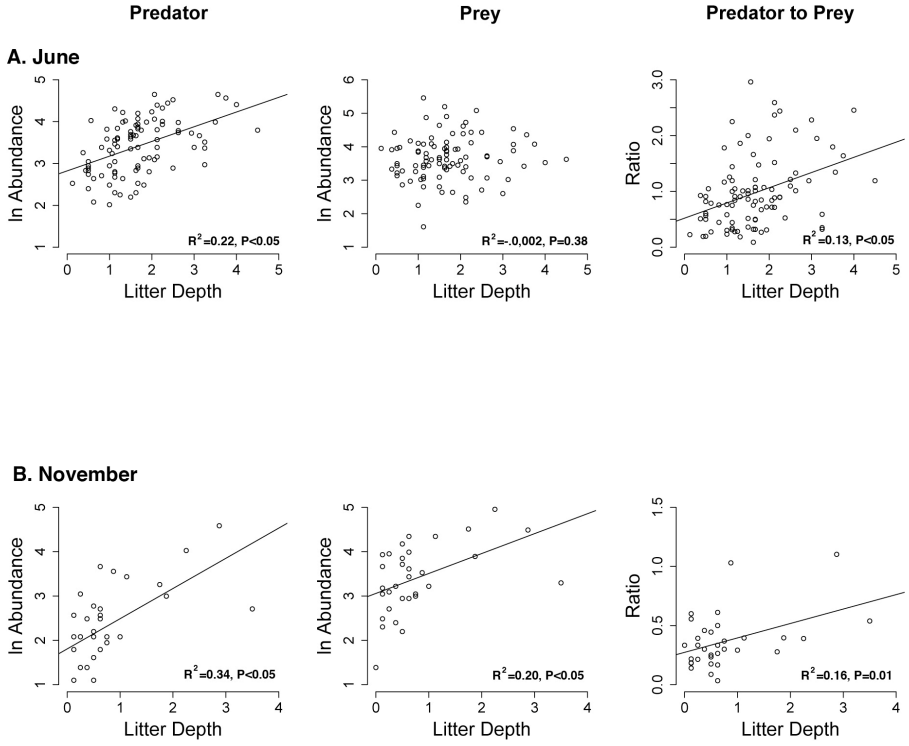

Figure 4.Chapter 2

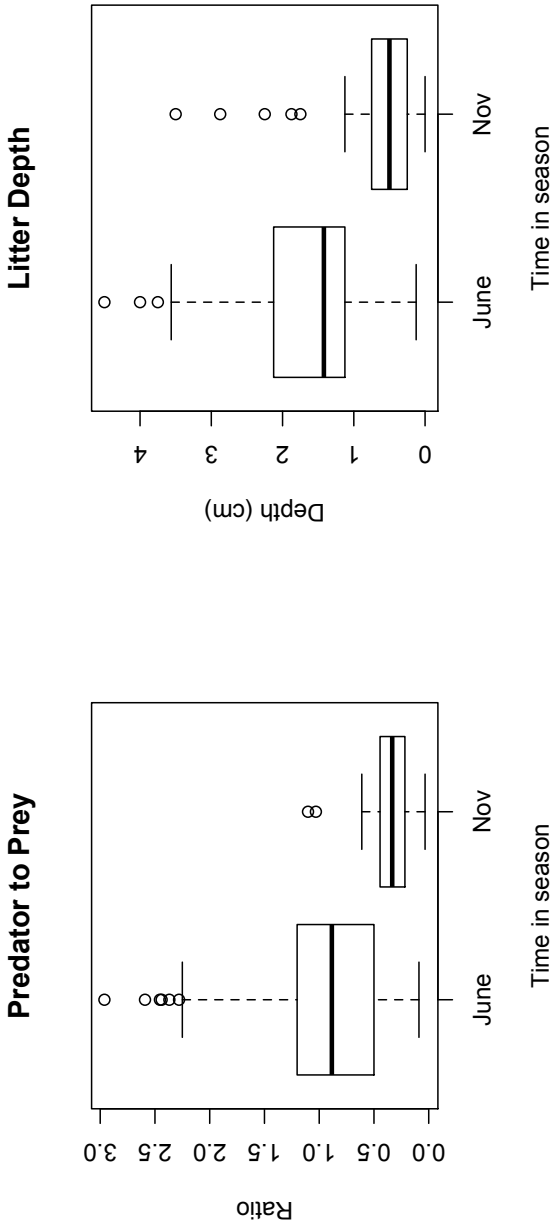

Figure 5. Chapter 2

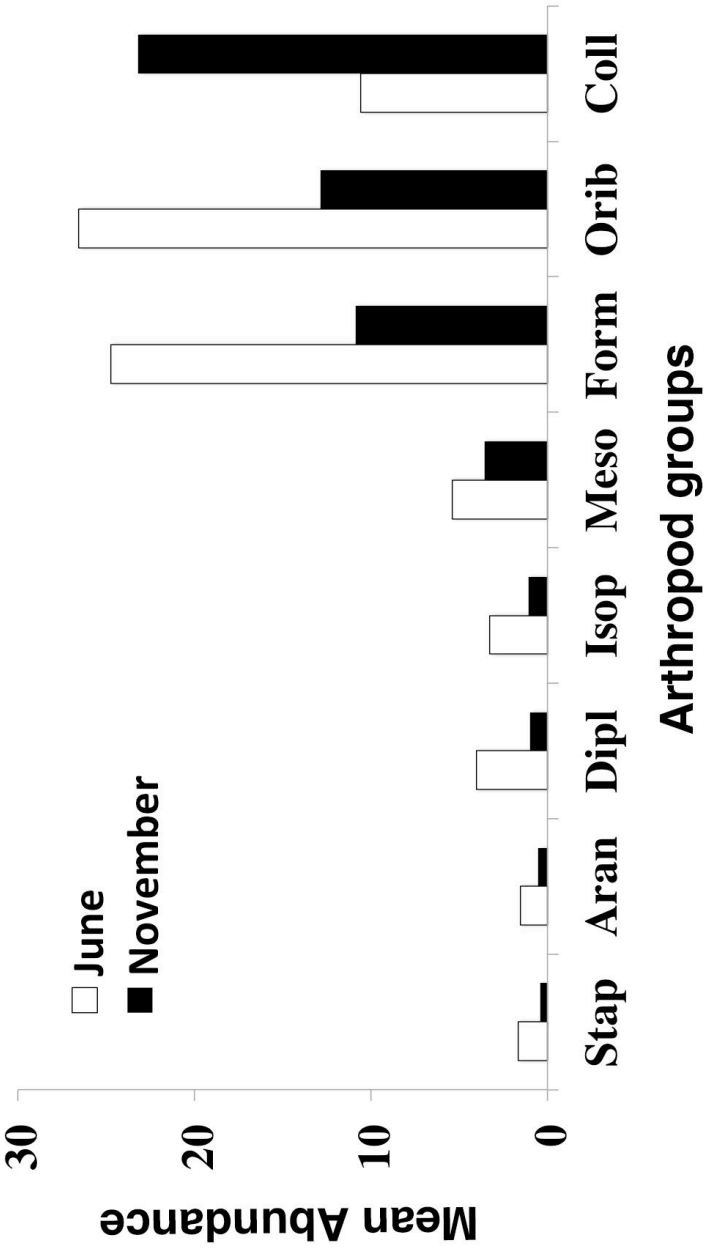

Table Legends. Chapter 2

Table 1. Working framework for possible scenarios of the Tree and Species Hypotheses. Expected outcomes and mechanisms for associations between BFW structure and plants

Table 2. Testing the Tree and Species Hypothesis. Results of ANCOVA for eight common arthropod taxa. The model included tree species as treatment and Distance (Tree Hypothesis) and Litter Depth (Species Hypothesis) as covariates. Values in bold are significant after Bonferroni correction ($p= 0.05/8 = 0.006$).

Table 3. Testing the Ecosystem Size Hypothesis as a mechanism for the Species Hypothesis. Results of ANCOVAs for Predators, Prey and Predator to Prey ratios. The model included tree species as treatment and Distance (Tree Hypothesis) and Litter Depth (Species Hypothesis) as covariates. Values in bold are significant at $p = 0.05$.

Table 4. Effect of seasonal variability on litter profiles across different tree species. G-tests of independence (Sokal and Rohlf 1995) test whether frequency of A) eight arthropod taxa used in this study and B) arthropod taxa grouped in three trophic levels (predators, omnivores and microbivores/detritivores) under tree species (all trees and by separate) were independent of season. All tests were significant.

Table 1. Chapter 2

	Species Hypothesis	
Tree Hypothesis	TRUE	FALSE
TRUE	- BFW structure changes with proximity to the tree, and across tree species - Niche Theory. BFW structure and diversity linked to tree diversity.	- BFW structure changes with proximity to trees. - Plants provide litter-based structural variability only.
FALSE	- BFW structure is correlated to plant diversity, but not tree effects are found - Trees and BFWs respond similarly to third factors (e.g., soil nutrients, topography)	- No association. BFW structure is independent of plant and plant-based resources. - Absence of coevolutionary processes between plant and BFW structure.

Table 2. Chapter 2

	TREE HYPOTHESIS				
TAXA		df	ss III	F	p
Araneae	Tree sp.	9	1.8	0.65	0.753
	Distance	1	2.1	6.85	0.010
	Residuals	172	53.4		
Collembola	Tree sp.	9	20.9	3.91	<0.001
	Distance	1	0.9	1.43	0.232
	Residuals	172	101.8		
Diplopoda	Tree sp.	9	9.3	1.60	0.118
	Distance	1	3.1	4.76	0.030
	Residuals	172	110.6		
Formicidae	Tree sp.	9	7.7	1.21	0.289
	Distance	1	3.8	5.40	0.021
	Residuals	172	120.7		
Mesostigmatids	Tree sp.	9	3.9	0.85	0.563
	Distance	1	1.1	2.26	0.134
	Residuals	172	86.3		
Isopoda	Tree sp.	9	14.4	3.24	0.001
	Distance	1	1.0	2.00	0.159
	Residuals	172	85.1		
Oribatids	Tree sp.	9	4.1	0.42	0.924
	Distance	1	2.3	2.13	0.146
	Residuals	172	186.2		
Staphylinid	Tree sp.	9	3.5	1.06	0.393
	Distance	1	0.1	0.15	0.691
	Residuals	172	63.4		

Table 2. Chapter 2 (Continuation)

	SPECIES HYPOTHESIS				
TAXA		df	ss III	F	p
Araneae	Tree sp.	9	3.5	1.64	0.117
	Litter depth	1	1.6	6.51	0.013
	Residuals	83	19.8		
Collembola	Tree sp.	9	12.1	2.85	0.006
	Litter depth	1	1.1	2.39	0.126
	Residuals	83	39.2		
Diplopoda	Tree sp.	9	2.3	0.48	0.880
	Litter depth	1	3.4	6.49	0.013
	Residuals	83	43.3		
Formicidae	Tree sp.	9	2.5	0.55	0.828
	Litter depth	1	3.8	7.55	0.007
	Residuals	83	41.4		
Mesostigmatids	Tree sp.	9	5.4	1.46	0.176
	Litter depth	1	3.3	7.87	0.006
	Residuals	82	33.8		
Isopoda	Tree sp.	9	6.0	1.55	0.144
	Litter depth	1	0.5	1.04	0.309
	Residuals	83	35.9		
Oribatids	Tree sp.	9	4.9	0.60	0.788
	Litter depth	1	0.1	0.13	0.713
	Residuals	83	74.5		
Staphylinid	Tree sp.	9	2.2	0.75	0.663
	Litter depth	1	3.4	10.34	0.002
	Residuals	81	27.0		

Table 3. Chapter 2

TREE HYPOTHESIS

		June				November			
		df	ss III	F	p	df	ss III	F	p
Predator	Tree spp.	9	4.5	1.03	0.422	4	11.2	4.20	0.005
	Distance	1	2.5	5.15	0.024	1	0.8	1.13	0.291
	Residuals	172	83.0			62	41.4		
Prey	Tree spp.	9	4.5	0.83	0.591	4	3.3	1.07	0.380
	Distance	1	1.8	3.03	0.084	1	5.4	6.89	0.011
	Residuals	172	104.8			62	48.1		
Pred:Prey	Tree spp.	9	7.2	1.02	0.424	4	2.4	2.87	0.030
	Distance	1	0.4	0.55	0.461	1	1.3	6.09	0.016
	Residuals	172	134.3			62	13.0		

SPECIES HYPOTHESIS

		June				November			
		df	SS III	F	p	df	SS III	F	p
Predator	Tree spp.	9	2.5	0.84	0.578	4	3.3	1.62	0.198
	Litter D.	1	9.5	28.98	<0.001	1	3.8	7.41	0.011
	Residuals	84	27.6			27	13.9		
Prey	Tree spp.	9	1.8	0.42	0.922	4	2.3	1.25	0.313
	Litter D.	1	0.9	1.99	0.162	1	2.0	4.37	0.046
	Residuals	84	39.3			27	12.3		
Pred:Prey	Tree spp.	9	1.1	0.32	0.967	4	0.2	0.86	0.499
	Litter D.	1	3.8	10.18	0.002	1	0.1	2.53	0.124
	Residuals	84	31.4			27	1.2		

Table 4. Chapter 2

A

	G	df	p
All trees	971.59	7	<0.001
Anacardium	354.86	7	<0.001
Astronium	313.25	7	<0.001
Cecropia	88.14	7	<0.001
Dendropanax	436.68	7	<0.001
Trema	140.91	7	<0.001

B

	G	df	p
All trees	155.63	2	<0.001
Anacardium	32.20	2	<0.001
Astronium	77.86	2	<0.001
Cecropia	8.40	2	0.015
Dendropanax	73.98	2	<0.001
Trema	37.29	2	<0.001

CHAPTER 3: THE ANT GENUS *TATUIDRIS* (HYMENOPTERA: FORMICIDAE) IN THE NEW WORLD

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Abstract

The taxonomy of the rare ant genus *Tatuidris* is revised by studying morphological variability among 118 specimens involving 52 collection events in 11 countries, and sequences of the cytochrome c oxidase subunit 1 (CO1 "DNA barcodes") of 28 specimens from 13 localities in six countries. *Tatuidris* comprise medium size, cryptic specimens of uniform habitus that inhabit the leaf litter of Neotropical forests from Mexico to French Guiana, central Brazil and Peru. Only one species, *T. tatusia*, is hypothesized to inhabit this broad geographic range. Male and gyne castes are described for the first time for the species.

Introduction

The genus *Tatuidris* comprises medium-sized, cryptic individuals of extremely uniform habitus that inhabit the leaf litter in the Neotropics (Brown and Kempf 1968, Fernández and Sendoya 2004). Workers of *Tatuidris* present a distinctive morphology (Figure 1-4), consisting of a shield-like head with a broad vertex, ventral-turned heavy mandibles which do not overlap at full closure, deep antennal scrobes with eyes at or close to their apex, compact and fused mesosoma, 7-segmented antenna, first gastral segment ventrally directed, and, unique among ants: an antenna socket apparatus sitting upside down on the roof of the expanded frontal lobe (first noted in Keller 2011, see his figures 12B and 12C). These characteristics, combined with a thick integument and a general rounded habitus, are reminiscent of armadillos. Both "tatuidris" and "tatusia" mean also "armadillo" and thus it has been proposed elsewhere the common name of "armadillo ants" for specimens in this genus (Longino, pers. com.; Lacau et al. 2012).

Taxonomy summary

Brown and Kempf (1968) raised *Tatuidris* to home the species *tatusia*. Due to morphological similarities, *T. tatusia* was included in what was then a myrmicine tribe, the Agroecomyrmecini. The tribe also includes two fossil genera, *Agroecomyrmex* Wheeler from the Baltic amber [44.1 My ago] and *Eulithomyrmex* Carpenter from the Miocene Florissant Shale of Colorado in North America [34 My ago] (Carpenter 1930, 1935; Moreau and Bell 2011). The systematic status of the tribe has been the focus of intense debate. In the original description, Brown and Kempf (1968) hypothesized similarities of the general habitus of *Tatuidris* with that of the dacetini *Glamyromyrmex*

(currently a junior synonym of *Strumigenys*) and *Phalacromyrmex*. However they concluded: “analysis of these similarities indicates […] that they are mostly convergent and not based on close phylogenetic relationship”. Further work by Bolton (1984) and Brown (1977) explored the similarities of *Tatuidris* with *Ishakidris* and *Pilotrochus,* respectively. These taxa share an expanded head vertex, deep antennal scrobes and a compact mesosoma, but again, these similarities were deemed convergent (Bolton 1984).

Bolton (2003) was the first to suggest the taxonomic instability of the genus within Myrmicinae and raised the armadillo ants to subfamily level. Diagnostic characters proposed by Bolton (2003) for the new subfamily Agroecomyrmecinae included: large mandibles with a mandibular masticatory margins that opposes at full closure but do not overlap; eyes at extreme posterior apex of deep antennal scrobes; clypeus very broadly triangular, broadly inserted between the frontal lobes; antennal sockets and frontal lobes strongly migrated laterally, far apart and close to lateral margins of the head, mesotibia and metatibia with pectinate spurs, short and compact mesosoma; a sessile petiole (in posterior view the tergite and sternite not forming a circle), an abdominal segment III (postpetiole) without tergosternal fusion (segment large and very broadly articulated to segment IV), a helcium in frontal view with the sternite bulging ventrally and overlapped by the tergite, an abdominal segment IV with a complete tergosternal fusion (coded incorrectly), with a stridulitrum on the pretergite. The sternite of abdominal segment IV is reduced, and the tergite is much larger than the sternite and strongly vaulted.

This subfamily rank of Agroecomyrmecinae was re-assessed by Baroni Urbani and de Andrade (2007). In their systematic account of the dacetine and basicerotine ants, they analyzed a relatively large morphological dataset (e.g. 54 characters from 24 terminal taxa) that included former dacetines, basicerotines, phalacromyrmecines and *Tatuidris* as well as other non-Myrmicinae taxa such as the Australian genus *Myrmecia* and the tropical genus *Pseudomyrmex*. Baroni Urbani and de Andrade (2007) was the first attempt to include the ant genus *Tatuidris* as terminal taxa in a cladistic analysis and supported the re-inclusion of the agroecomyrmecines in the ant subfamily Myrmicinae close to the tribe Dacetini. At least six morphological synapomorphies (Baroni Urbani and de Andrade 2007:78) bringing *Tatuidris* back into the subfamily Myrmicinae included: mandibles at rest opposing at least in part (instead of crossing), an MTI (mandibular-torular index) < 130; reduction of maxillary palps from 2-jointed to 1-jointed; reduced male mandibles, presence of a two-segmented antennal club; and a reduced number of antennal joints. Two uniquely derived characters (i.e. autapomorphies; a differently shaped petiolar tergum and sternum and the eyes at or close to their apex) separated *Tatuidris* from all other extant ant genera included in their study (Baroni Urbani and de Andrade 2007).

Differing with morphology-based phylogenetic studies, molecular evidence suggests that to the long held view of agroecomyrmecines close to Myrmicine is not probable. Molecular analyses of the internal phylogeny of the ants (Brady *et al.* 2006, Moreaux *et al.* 2006, Rabeling *et al.* 2008) usually associate the agroecomyrmecines to the ‘poneroid’ group of subfamilies, specifically, close to the Paraponerinae, and give support for the exclusion of the genus from the Myrmicinae, in the ‘formicoid’ clade

(Ward 2009). Given the early appearance of the Agroecomyrmecinae in the geologic record, the similarities of these ants to the myrmicines are assumed to appear by convergence and/or retention of plesiomorphic forms (Ward 2011). Recently, the phylogenetic relationships of the poneromorph subfamilies (including *Tatuidris)* were challenged by Keller (2011). This study included a large set of taxa and morphological characters, several of them coded and illustrated for the first time. Interestingly, *Tatuidris* was again grouped close to Myrmicinae, but surprisingly, the Myrmicinae nested inside the poneromorphs (Keller 2011).

Justification for a taxonomic revision

Since its description, more than 40 years ago, no modern morphologically systematic account of *Tatuidris* has been given. This has produced the accumulation of several *Tatuidris* specimens in regional ant collections and country inventory lists (Bolton 1984, Rojas 1996, Vasconcelos and Vilhena 2003, Fernández 2002, Vieira 2005) attributable to potential morphospecies (Longino *et al*. 2002) and species (Lacau et al. 2012). In the present work, I primarily review specimens from *Tatuidris* gathered from several different localities throughout the Neotropical region, describe morphological variability encountered across this range, and describe for the first time the gyne and male caste for the genus. While I present here descriptions of morphological characters for male and females, with enormous phylogenetic value, I do not discuss their implications for the evolutionary history of *Tatuidris*.

Materials and Methods

Tatuidris is a rare genus. The primary sources of specimens in this study are museum collections and specimen loans. When travel or material loans were not feasible, specimens were analyzed from pictures. But efforts were made to review type material. In total, this study comprises 118 specimens from 52 collection events (proportion of specimens to collection events is around 2.26 and the average number of collection events per country is only 4.3). Several specimens included in this study have been imaged and are available on AntWeb (www.antweb.org) or at the MCZC (Gary Alpert). Specimens studied here come from the following ant collections:

CASC	California Academy of Sciences, San Francisco, USA.
INBC	Institute of National Biodiversity, San José, Costa Rica.
INSPA	Instituto de Pesquisas da Amazônia in Manaus, Amazonas, Brazil.
IEXM	Instituto de Ecología A.C. de Xalapa, Mexico.
MCZC	Museum of Comparative Zoology, Harvard University, Cambridge, USA.
MEKC	Michael E. Kaspari Lab Collection.
MUSM	Museo de Historia Natural "Javier Prado, " Universidad Nacional Mayor de San Marcos, Lima, Perú.
MZSP	Museu de Zoologia, Universidade de São Paulo, São Paulo, Brazil.
QCAZ	Museo de Zoología de la Pontificia Universidad Católica del Ecuador. Quito, Ecuador.
WEMC	William and Emma MacKay Collection. El Paso, Texas, United States.

Observations were made at 66x on a Zeiss Stem SV11 dissecting microscope and at 90x in an Olympus SZX12 dissecting microscope; measurements were taken to the nearest 0.01 mm. Male nomenclature follows Yoshimura and Fisher (2007 and 2009). Wing venation follows Serna et al. (2011). Measurements and indices are described as follows:

AScL. Antennal scrobe length, from the anterior angle to the middle of the apex-near eye.

AScW. Width of antenna scrobe at its widest.

EL. Length of compound eye, at its widest.

FFS. First funicular segment (male and queen only).

FL. Fore femur length, excluding the condylar bulb.

FW. Fore femur width, at its widest.

HL. Head length, measured with head in full-face view, from the anterior median clypeal border (not including the lamellate apron) to the median posterior border.

HW. Head width, measured with head in full-face view. The measure is taken anteriorly to the eyes, where the antenna carina starts. In workers and gyne, HW does not include the eyes. In male, HW includes the eyes.

IAD. Inter-antenna distance. This measure is taken in full-face view. In most workers (and gyne), the antenna fossa lies in upper side of cranium and is visible (as a translucent cavity) across the heads cuticle.

PL. Petiole length, measured along line parallel to tergosternal suture, from anterior-most to posterior-most visible portions of tergite.

PW. Petiole width, in full dorsal view.

PpL. Postpetiole length, measured along line parallel to tergosternal suture, from anterior-most to posterior-most visible portions of tergite.

PpW. Postpetiole width, in full dorsal view.

PrW. Pronotum width, in full dorsal view.

ScapeL. Scape length. Because the antenna inserts upside-down, the antenna bulb can be easily seen in full-face view. This measure is taken from the middle of the antennal bulb to the posterior edge of the scape.

ScapeW. Scape width at its widest.

TiL. Hind tibia length.

TiW. Hind tibia width.

WbL. Weber's length, in lateral view, from the base of anterior slope of pronotum to the lower posteroventral angle of propodeum.

WingL. Wing length (male and queen only).

Indices

CIx. Cephalic index (HW × 100/HL).

PPpIx. PW*100/PpW

REL. Relative eye size (EL × 100/HL).

ScapeIx. Scape index (SL/HWx100). (not yet)

Morphometric analysis

Patterns of morphological variation were summarized with a Principal Component Analysis (PCA). The PCA was done on the correlation matrix of 14 morphological variables (AScL, AScW, EL, HL, HW, IAD, PL, PpL, PW, PpW, PrW, TiL, TiW, WbL) and 37 specimens (that included 4 different pilosity patterns) for which all variables were measured. The correlation matrix gives equal weights to all morphological variables without regard to their relative size. PCAs explaining more than 1% of the variation were retained. In general, I interpreted principal component-1 (PC-1) as summarizing the variation in size magnitude among specimens. Variation summarized by PC-2, PC-3 and PC-4 was interpreted as shape variability.

DNA Barcode Analysis

CO1 DNA barcodes for specimens were obtained in collaboration with the Biodiversity Institute of Ontario and the Barcode of Life Database (BOLD, Ratnasingham and Hebert 2007). Samples used for molecular analysis came mostly from dry specimens at museum collections. Usually, hind legs were removed from specimens and sent for analysis to BOLD. DNA extraction, PCR, and sequencing reactions followed the procedures described in Herbert et al. 2003 and Fisher and Smith 2008. Only sequences greater than 500 bp were included in analyses. Collection data, sequences, and GenBank accession numbers (XXX – XXX) are available in Supplement File 1, and in the project 'TATU − Tatuidris of the Neotropics' publicly available at http://www.barcodinglife.org. An additional COI sequence for *T. tatusia* (Moreau et al. 2006) and four outgroup ant taxa (i.e. *Paraponera clavata, Proceratium*

avium, Probolomyrmex sp.*,* and *Strumigenys coveri*) were extracted from GeneBank. Recently, *P. clavata* has been recalled as the closest, sister, taxa to *Tatuidris* (Moreau et al. 2006, Ward 2011). To assess the discriminatory power of CO1 barcodes, we calculated sequence divergence using Kimura 2 parameter distance model (K2P) and build a Neighbor Joining (NJ) tree using MEGA version 5.1 (Tamura et al. 2007). Support for tree branches were calculated using 999 bootstrap replicates. Because preliminary integration of morphology and CO1 DNA barcode results suggest that only 'one' species is present among the studied material, I avoided a more comprehensive analysis of DNA barcode sequences (e.g. species specific diagnostic nucleotide positions, and analysis of DNA barcode 'gaps' [comparisons of intra vs. inter-species genetic distance]).

Results

Genus *Tatuidris* (emended)

Tatuidris Brown and Kempf 1968: 183. Type species: *Tatuidris tatusia* Brown and Kempf 1968: 187, by monotypy.

Worker: Size small. Body short and compact. Color ferrugineous to dark red. Integument thick and rigid. HEAD. Head shape piriniform, broadest behind. Maxillary palps one-jointed. Labial palps two-jointed. Labrum bilobed, broader than longer, capable of full reflexion over the buccal cavity. Mandibles opposing in most of their border (except in the tips of the masticatory margin). Masticatory margin with two blunt

apical teeth overlapping at closure. Setae (mandibular brush) abundant, present in the ventral side of mandibles. Antennal joints 7-segmented. Antennal club two segmented, well developed. Scape clavate, gently down curved at base. Torulus with hypertrophied dorsal lobe and strongly curve downwards. Antennal scrobe present. Antennal socket and antennal scrobe confluent. Antenna socket apparatus sitting upside down on the roof of the expanded frontal lobe. Eyes present, size medium, located laterally at antennal scrobes posterior border. ALITRUNK. Promesonotal suture fused. Metapleural gland orifice round. Metapleural gland opening visible. Metapleural gland bulla separated from annulus of propodeal spiracle more than the diameter of the spiracle. Katepisternal oblique groove absent. Lower mesopleura marked, with longitudinal costulae. Propodeum unarmed. Propodeal spiracle, in profile, located at about mid-length of sclerite. PETIOLE and POSTPETIOLE. Petiole short and sessile. Petiolar ventral process large and rounded. Petiole dorso-ventrally fused. Petiole in posterior view with tergum and sternum differently shaped without tergum and sternum equally convex, forming a circle. Postpetiolar tergum and sternum overlapping at junction. Postpetiole in dorsal view wider in posterior half. GASTER. Articulation between postpetiole and gastral segment 1 (abdominal segment 4) broad. Postpetiolar presclerites not set in a concavity or depression. Pretergite of first gastral segment with neck-like constriction. Stridulitrum present on first gastral segment. Limbus (i.e. anterior transverse cuticular ridge of the first gastral segment) absent. Suture between first gastral tergite and sternite anteriorly rounded. First gastral tergosternal union strong, but not fused. Base of the first gastral sternum in profile rounded. First gastral sternite length is reduced, such that tergite is much larger than the sternite and strongly

vaulted. First gastral tergum and sternum smooth or with scattered punctuate. LEGS. Mid and hind tibial spurs present..

Gyne. Size medium. Body short and compact, with exterior morphology and characters similar to workers. Body covered by hairs. Color light. Integument thick and rigid. HEAD. Head shape piriniform, broadest behind. Vertex straight, not concave. Labrum bilobed, broader than longer, capable of full reflexion over the buccal cavity. Mandibles opposing in most of their border (except in the tips of the masticatory margin). Masticatory margin with two blunt apical teeth overlapping at closure. Mandibular setae, present but less abundant than in workers. Antennal joints 7-segmented. Antennal club two segmented, well developed. Scape clavate, gently downcurved at base. Antennal scrobe present. Antennal socket and antennal scrobe confluent. Antenna socket apparatus sitting upside down on the roof of the expanded frontal lobe. Eyes present, size big, located laterally at antennal scrobes posterior border. WINGS. Large, about 60% larger than total body length. Forewing well developed, with costal cell, basal cell (radial), sub-basal cell (cubital), no vein present between sub-marginal cell 1 and sub-marginal cell 2, R1 vein surrounding sub-marginal cell 3, discal cell 1 and discal cell 2 present, divided by cubital vein which extend a distance similar to the inferior edge of discal cell. Hindwing well developed, with Cu-a vein present. Basal cell completely surrounded by M-Cu and and rs-m+M veins. ALITRUNK. Promesonotal suture present, not fused. Scutellum broad. Anepisternum and katepisternum broad and shiny, not sculptured. Propodeum armed with a small posteriorly directed spine. Propodeal spiracle in profile at about one-diameter from posterior edge. Metapleural

gland present, metapleural spiracle big, longer than broader, within a dorsally directed fold. PETIOLE and POSTPETIOLE. Both petiole and postpetiole similar in shape to worker's petiole and postpetiole. Petiole broadly attached, not dorsally, to abdominal segment III. Abdominal segment III (Postpetiole), in lateral view, much shorter than abdominal segment IV. GASTER. Shiny. Vaulted. Constriction between Abdominal segment III and abdominal segment IV present. Abdominal sternun IX, simple, triangular in shape, without spines or lobes. Sting present. LEGS. Mid and hind tibia with pectinate spurs present.

Male: Size small. Body short and compact, with exterior morphology (except head) similar to workers. Body covered by decumbent setae. Color dark. HEAD. Dorsum with scrabrous-strigate sculture. Lateral ocelli and median ocellus present. Antenna long 12-segmented. Antennal sockets located at dorsum, at mid-length from the anterior border. Antennal scrobes absent. Antennal carinae absent. Scape very short about 1.3 times as long as pedicel segment. First flagellar segment relatively short, about the same length as second antennal segment, slightly curved towards the base. Antennal club absent, but apical segment is at lest 2 times longer than preceding segment. Mandibles reduced, falcate, with no characteristic masticatory and basal margins. Mandible edentate, with no visible apical tooth. Clypeus broad, with straight anterior margin. Clypeus does not extent to space between eyes. Eyes large, located at mid-length at lateral margin. WINGS. Large, about 50% larger than total body length. Venation and cell composition of both fore- and hind-wings are similar to that of the gyne. ALITRUNK. Oblique mesopleural furrow close, but not reaching, the pronotum. Mesonotum notauli absent.

Mesoscutum and mesoscutellum mostly shiny, with small fovea. Pronotum with rugae. PETIOLE and POSTPETIOLE. Constriction between abdominal segment II (petiole) and abdominal segment III (postpetiole) present. Petiole and postpetiole similar in shape to worker's petiole and postpetiole. Petiole broadly attached, not dorsally, to postpetiole. Postpetiole, in lateral view, much shorter than abdominal segment IV. GASTER. Shiny. Vaulted. Constriction between postpetiole and abdominal segment IV present. Abdominal sternun IX, simple, triangular in shape, without spines or lobes. LEGS. Hind tibia with 1 pectinate spur.

Tatuidris tatusia Brown and Kempf 1968 (revised)

Tatuidris tatusia Brown and Kempf 1968: 187, Figure 1. Holotype and Paratype workers: El Salvador, La Libertad, 2 mi S. Quetzaltepec ,VII-17-1961, (M.E. Irwin leg.) Holotype (LACM), Paratype (MCZC) [examined].

Tatuidris kapasi Lacau and Groc 2012: 2, Figures 1 to 6. Holotype worker: Guyane Francaise, Montagne de Kaw, 04◦ 38.21′ LN; 052◦ 17.36′ LW, Alt. 260 m., ix.2008, (S. Groc, A. Dejean, and B. Corbara leg) (CPDC) [examined by picture only] *n.syn.*

Worker, male and gyne diagnosis: With same characters as in the genus description.

Justification for the synonymy

A comprehensive analysis of the description of *T. kapasi* suggests that the morphological characters of this specimen lie within the continuous variability encountered in *Tatuidris* across the Neotropics. Two considerations were taken, first the description of *T. kapasi* rely on a relatively large specimen where sculpture and body proportions usually vary the most. Second, the type locality of *T. kapasi* lies at the extreme of *Tatuidris* geographic distribution. See also discussion on morphological and molecular analysis below.

Pilosity variability

Currently, four striking pilosity patterns are known to occur within *Tatuidris* collections (Figure 5). Pilosity pattern A (Figure 6) consists of abundant long flexuous setae and shorter appressed setae. This is the pilosity pattern that most resembles the type specimens from El Salvador. Pilosity pattern B (Figure 7) consists of uniform decumbent setae arrayed constantly through the head, mesosoma, petiole, postpetiole and gaster. Pilosity pattern C (Figure 8) is characterized by dense lanose pubescence. Pilosity pattern D (Figure 9) is characterized by a shiny and smooth body with short appressed, never long or erect, setae scattered throughout the body. Setae length can vary but setae counts never surpass more than 150 setae in half of the head.

CO1 DNA barcodes

In total, 28 sequences (20 of them with full, 658bp, length) of the COI barcode gene, out of 69 specimens sent to the laboratory, were recovered and included in the

analyses. 120 out of the 658 basepairs (18.23%) were variable. In general, specimens (excluding colony duplicates) presented very high levels of intraspecific pairwise differences (average = 5.36%, min = 0%, max=15.08%). These percentages are well above the 2% usually recovered in DNA barcode literature in general (Ratnasingham and Hebert 2007), and for ants (Smith and Fisher 2009, Jansen et al. 2009). Pilosity patterns present among our individuals were not in similar specimen clusters based on Neighbor Joining K2P similarities (Figure 10). Four different preliminary groups were present (G1, Mexico+Honduras+Guatemala; G2, Costa Rica + Nicaragua; G3, Ecuador (West of Andes); G4, Ecuador (East of Andes/Amazon Basin). Furthermore, across this geographic gradient, which include one continental divide (Mexico, north of) and one mountain range (the Andes), pairwise divergence was significantly related to distance (R^2=0.37, $p<0.01$, Figure 11).

Size

Specimens of *T. tatusia* are small (average WbL = 0.62mm), but specimens can vary greatly in size, with biggest specimens being some twice as big as the smaller ones (min. WbL=0.45 mm, max.WbL=0.90 mm). Size variability within trap catches (possibly same colonies) may be considerable. For example, workers from one collection catch collection in Nicaragua (collection series MGM#1179) varied 30% in size (WbL from 0.65 to 0.85 mm). Our PCA analysis revealed that most variability among specimens is related to size (proportion of variance explained, PC-1 = 0.915), with PC-2, PC-3 and PC-4 (e.g. shape) explaining little (0.033, 0.021 and 0.011, respectively) of total variation (Table 1). Eye length contrasted against all other

variables in PC2, and tibia length and tibia width contrasted against all other variables in PC3 (Table 1). Size variability summarized in the PCA was not related to pilosity patterns. In general no PC correlated with pilosity patterns (Figure 12)

Sculpture

The strength and depth of all sculpture patterns is accentuated in larger sizes. Collections from Nicaragua also tend to present more accentuated sculpture patterns. Head dorsum is usually smooth and shining, except for the area below eyes, which presents longitudinal carinae. Head vertex covered with transverse carinulae; lateral surface of mandibles smooth and shining except for longitudinal superficial striae on sides that vary in depth; antennal scape shagreened and superficially areolate; superficies of ventrolateral part of pronotum vary strongly across specimens, from smooth and shining to strongly striate, or carinulate; dorsum of mesosoma with concentric carinulae, sometimes slightly punctate; mesopleuron smooth and shining except for punctuations and areolae on ventral margin; propodeal declivity smooth with fine transverse striae; petiole and postpetiole dorso-laterally strigulate. Gaster mostly smooth and shiny but sometimes finely and sparsely strigulate.

Distribution

The genus *Tatuidris* is restricted to the Neotropics, but it has an ample distribution that spans from Central Mexico to Central Brazil, French Guiana (Lacau et al. 2012) and Amazon of Peru (Figure 13). No collections are known from the Caribbean, Galápagos or other islands. Most specimens and collections are currently

known to occur in localities west of Los Andes, with more collections tending to occur towards Central America and Mexico. Most collections come from mountainside (pre-montane) areas at mid elevations (usually 800-1200m of altitude). Collections from lowland Amazonia are few.

Natural history

Little is known about the biology of the ant genus *Tatuidris* and until recently no observations of live specimens were registered. Details of a first collection event of a small live colony (3 workers and 4 gynes) by Dr. Thibaut Delsinne in a mid-elevation forest in Southeastern Ecuador suggest that *Tatuidris* may well be a highly specialized predator, as colonies kept in captivity did not accept any food item offered to them. Food items rejected by the ants included: live and dead termites, millipedes, mites, various insect parts, sugar/water, tuna, biscuits, live and dead fruit flies (Drosophila), live springtails, live myriapods (Chilopoda and Diplopoda), live and dead Diplura, small live spiders, small live pseudoscorpions, one small snail, hen egg, ant larvae (*Gnamptogenys* sp.), live ant workers (*Cyphomyrmex* sp., *Brachymyrmex* sp.). Potential food items (arthropods) for *Tatuidris* were taken from soil samples and Winkler samples (following Silva and Brandão 2010) collected at the site where *Tatuidris* was *a priori* determined abundant.

Further observations by T. Delsinne suggest that *T. tatusia* may be a sit-and-wait predator, as "both workers and queens moved very slowly and were very clumsy. They often remained motionless during several tens of seconds or even several minutes when

disturbed (either by my handling or by the contact with another arthropod). It is difficult to see them as powerful predators!" (pers. com.). Besides, these observations were mainly done at night, suggesting that *T. tatusia* may have nocturnal habits. Collection patterns also suggest that *T. tatusia* may be a nocturnal species. For example, in the Río Toachi forest of Ecuador *T. tatusia* specimens tend to fall in pitfall traps, instead of Winkler sacs (Donoso and Ramón 2009). Because pitfall traps usually work 24-h, but Winkler sacs generally uses litter sifted during the day, then ants with nocturnal habits may be underrepresented in Winkler samples. Both small eyes and the lack of daylight field observations of the genus are in accordance with this speculation.

Other

Eye relative position is highly variable within the species. For example, eye location ranges from being completely within the antennal scrobes to completely outside the scrobes (Figure 1b). In some cases (specimen J.Longino#2088-S) the eye itself is located outside the antennal scrobe, but the eye's fossa is well marked and confluent with the antennal scrobe. In specimens from Nicaragua (specimens from MGB1179 colony collection), a strongly impressed antennal carina forms (the carina is usually weakly impressed in all specimens) bifurcates from the antennal scrobes and lies straight above the eye. In these specimens about 40% of the eye's area lie within the antennal scrobes. In the queen, only ~1/6 of the eye lies 'within' the antennal scrobes. A depression sometimes forms in the integument in the sides of the propodeum, below the propodeal spiracle and above the metapleural gland. The depth of this depression varies among specimens and tends to be deepest in larger specimens.

Worker measurements (in mm) and indices: (average (min–max) of no more that 46 specimens): AScL 0.46 (0.31, 0.67); AScW 0.24 (0.18, 0.36); CIx 129.03 (117.07, 137.93); EL 0.05 (0.03, 0.08); FL 0.43 (0.31, 0.70); FW 0.11 (0.08, 0.17); HL 0.59 (0.43, 0.88); HW 0.76 (0.56, 1.10); IAD 0.36 (0.25, 0.54); PL 0.16 (0.10, 0.24); PpL 0.16 (0.10, 0.25); PW 0.25 (0.18, 0.37); PpW 0.36 (0.26, 0.53); PPpIx 68.92 (58.14, 80.00); PrW 0.52 (0.38, 0.77); TiL 0.35 (0.27, 0.52); TiW 0.10 (0.06, 0.17); WbL 0.62 (0.45, 0.89); ScapeL 0.42 (0.32, 0.51); SccapeW 0.13 (0.11, 0.17); ScapeIx 329.82 (300.00, 360.00); Ant8 0.31 (0.25, 0.35).

Gyne measurements (in mm) and indices: AScL 0.47. AScW 0.15. EL 0.20. FFS 0.09. FL 0.77. FW 0.20. HL 0.88. HW 1.28. IAD 0.56. Pl 0.22. PPL 0.28. PPW 0.72. PW 0.45. TL 0.69. TW 0.20. WingL 4.60. WbL 1.53.

Male measurements (in mm): EL 0.32. FFS 0.13. HL 0.66. HW 0.88. IAD 0.21. ScL 0.11. WingL 3.6. WbL 1.22. FL 0.9.

Specimens examined

BELIZE: 2.5 millas S Belmopan, B-242, 4-Aug-1972, S. and J. Peck, Limestone forest, ex: Berlesse [MCZC]. Caves Branch, S. and J. Peck B-248, 4-14-Aug-1972, hi canopy forest, ex: Berlesse [MCZC]. BRAZIL: Amazonas, Manaus, Universidade do Amazonas, 2 workers, 16-Aug-2001, 03° 05' 36" LS, 59° 57' 52" LW, Evenlyn Pereira Franken, Terra Firme: Plato, ex: Pitfall [IMPA]. COLOMBIA: Magdalena, El

Campano, 2 workers, P. S. Ward # 7891-9, a-b, 13-Ago-1985, 1300m, 11° 07' LN, 74° 06' LW, montane rainforest, ex: sifted litter (leaf mold, rotten log) [QCAZ]. COSTA RICA: Alajuela, Casa Eladio, Rio Peñas Blancas, 4 workers, JTL1579-s, 26-Abr-1987, 800m, 10°19' LN, 84°43' LW, Wet forest, ex: Sifted leaf litter [INBC]. Heredia, 16km SSE La Virgen, 6 workers, Transect 11/WF/02/04-INBio-OET-ALAS transect, 17-Mar-2001, 1100m, 10°16'LN, 84°05'LW, ALAS, None, [INBC]. Heredia, La Selva Biological Station-2, 2 workers, Mayo/Junio-1996, 09°09' LN, 079°51' LW, Michael Kaspari [MEKC]. Puntarenas, Rio San Luis, 2 workers, JTL2088-s, a-b, 18-May-1988, 850m, 10°17' LN, 84°48' LW, Moist forest, ex: Sifted leaf litter on ground, [INBC]. ECUADOR: Cotopaxi, 19 km ENE La Maná, P. S. Ward # 11418-6, a and b, 10-Aug-1991, 1100m, 00°53' LS, 79°03' LW, Second-Grown Rainforest, ex: Sifted leaf litter and logs [MEKOU12093, Barcoded][QCAZ]. Pichincha, R.B. Maquipucuna, 2 workers, R. Anderson #99-208-6-8, 27-Oct-1999, 1200m, 00º07'00"N, 78º38'06W, Montane evergreen forest [QCAZ]. Pichincha, Unión del Toachi-Otongachi, many workers, 850m, 00°21'05" S, 78°57'10" W, Donoso and Vieira, Bosque Secundario, Pitfall [MEKOU12083, MEKOU12084 and LL4-P3-W1, Barcoded] [QCAZ]. Zamora-Chinchipe province: Zamora: Bombuscaro: Podocarpus National Park, evergreen premontane rainforest, 950m, coll. M. Leponce, 2007, spm# 33796, -4.115, -78.968, Winkler sample [QCAZ]. Zamora-Chinchipe province: Zamora: Bombuscaro: Copalinga private reserve, 1000m, secondary evergreen premontane rainforest, coll. T.Delsinne and T. Arias-Penna, 21.iv.2010, spm#4130219, -4.091, -78.961, Winkler sample [QCAZ]. GUATEMALA: Peten, Parq. Nac. Tikal, 270m, Tropical Moist Forest, M.G.Branstetter [Picture only, ANTWEB]. HONDURAS: Comayagua , PN Cerro Azul

Meambar, 1140, Cloud Forest, M.G.Branstetter [Picture only, ANTWEB]. MEXICO: Chiapas, 12 mi NW Ocozocoautla, 4-5 Sep - 1973, 400m, A. Newton, ex: Berlesse [MCZC]. Chiapas, 6km SW Ocosingo, CASENT0603397, R. Anderson # 91-116, 22-Sep-1991, 1400m, 16.867221, -92.0787132, Forest litter, ex:Berlesse [Picture only, ANTWEB]. Chiapas, MGB856, 860m, 16.980, -91.586, Mesophyll forest [QCAZ]. Chiapas, Lago Metzabok, 575m, 17.124, -91.636, Lowland wet forest [QCAZ]. Tamaulipas, El Cielo, 3 workers, 870m, 23.276, -99.276, M.G.Branstetter #1465a-1465c [QCAZ]. Oaxaca, Mirador Grande, 1 worker, 990m, 17.89844, -96.36253, M.G.Branstetter #1405 [QCAZ]. Veracruz, Los Tuxtlas, Ejido-López Mateos, 12 workers, Dic-2003, 50m, 18°24'56"LN, 94°56'53"LW, Patricia Rojas, Selva alta perennifolia, ex:Winkler [IEXM]. Veracruz, Los Tuxtlas, Volcán S. M. Pajapan, 847d, 04-Nov-1991, 510m, 18°16'00"LN, 94°46'71"LW, A. Cartas, Selva mediana subperennifolia, ex: Berlesse [IEXM]. NICARAGUA: Matagalpa, RN El Musún, 4.8km NNW Rio Blanco , 5 workers, 11-Nov-2008, 1170m, 12º 58.4′ LN, 085º 14′ LW; , M.G.Branstetter #1179a-1179e, mesic forest, ex sifted leaf litter [QCAZ]. PANAMA: Chiriqui, 20.4 Km North San Felix, R. Anderson # 17768_1, 08-Jun-1995, Wet mountain forest, ex: Litter sample [WEMC]. Chiriqui, Alto Lino, CASENT 0102681, 23-Jun-1965, 3800, Herman G. Real [CASC][Male]. Chiriqui, La Fortuna, Finca La Suisse, 35 Workers, R. Anderson, 11-Jun-1995, 1200m, Oak forest Litter [WEMC]. PERU: Cuzco, La convención Province, 4 km S Camisea River. Campamento Cashiriari-2, Plot 1, MUSM-ENT 0201599/ANTWEB-CASENT 0178882, WinklerTrap #38, 17-Jun-1997, 579m, 11°51'51.3" LS, 72°46'45.6" LW, J. Santisteban et al., Primary Rainforest, hilly terrain, ex: Winkler Trap [MUSM].

Discussion

More than 40 years after the original description by Brown and Kempf (1968), *Tatuidris* remains a remarkable and rather unknown ant genus. Here I hypothesize the presence of only one species, i.e. *T. tatusia*, among the specimens I have reviewed. I base this hypothesis on analysis of both morphological and COI DNA barcode variability. The morphological analysis presented here suggests that most size variability encountered among specimens is continuous, a fact that will likely continue hindering species delimitations. I also describe differences on pilosity and pubescence patterns I have encountered within collections. While this approach is not unique within ants and pilosity patterns have been used before to separate species in ant genera like *Myrmecocystus* (Snelling 1976), *Formica* (Mackay *et al.* 1988), *Rogeria* (Kugler 1994) and *Linepithema* (Wild 2008), I conclude that pilosity patterns do not offer good species-level differentiation in *T. tatusia*. Other meristic and continuous characters (size and shape of the body, coloration, sculpture) between the material examined are extremely uniform (or too variable) and currently do not offer a clear separation of specimens into species. Nonetheless, I am aware that the addition of new data (e.g. molecular, behavioral, internal anatomy, etc.) or better analytic methods and new collections of gynes and males may improve the species delimitation I propose in this work.

Molecular analysis based on DNA barcodes presented a pattern more difficult to explain. The intraspecific variability among individuals in 7 times larger than usually encountered among species (i.e. 2%, Ratnasingham and Hebert 2007, Smith and Fisher

2009, Jansen et al. 2009), and suggests that several cryptic species remain to be described. Within ants, analysis of DNA barcode data has proved a valid tool to delimit species (Smith *et al.* 2005, Fisher and Smith 2008), although this has not always been the case (Jansen et al. 2009, Wild 2009) and species delimitations always benefit from analysis of additional genes [e.g. wingless (WG), Elongation Factor 1-α (EF1-α), long-wavelength rhodopsin (LWR) and internal transcribed spacer (ITS-1 and ITS-2); Fisher and Smith 2008, Wild 2009, Nieukerken *et al.* 2012]. While this level of intraspecific variability should be enough to separate specimens into, at least, four species, I avoided doing it for two reasons. First, no clear morphological separation among putative DNA barcode groups is recovered from either a) the PCA analysis, or b) the distribution of pilosity patterns in the NJ tree. Naming species that are recognizably only by laboratory/molecular techniques will likely result in taxonomic confusion. Second, genetic distances among specimens are highly correlated with geographic distance, and the specimen less genetically similar (e.g. a single specimen from East of the Andes) separated by mountain chain. This high correlation between geographic and genetic distance is in opposition with general predictions of speciation across large geographic ranges. Future research on the biology and species boundaries within this genus will certainly be exiting.

The phylogenetic position of *Tatuidris* within Formicidae remains a challenging work. For example, a recent revision of the ponerine group of subfamilies by Keller (2011) provides new evidence for a rearrangement of internal phylogeny of Formicidae that differ from both molecular and traditional morphological approaches. One morphological autapomorphy for *Tatuidris* described by Keller (2011) was the position

of the antennal socket, which, in this genus, sits upside-down on the roof of the frontal lobe. Such position of the antennal sockets is easily recognizable when ants are with head in full face as small “blisters”. A closer examination of this character among other ant genera suggests that *Phalacromyrmex*, an ant genus traditionally associated to *Tatuidris*, may present this character as well (Figure 14; see also similarities in habitus presented by males of these two genera). Here I hypothesize that further re-examination of this character as well as analysis of molecular characters of *Phalacromyrmex* will likely shed light to the origin and phylogenetic status of *Tatuidris*.

Figure Legends. Chapter 3

Figure 1. SEM images of *Tatuidris tatusia* external morphology. A) Head in (partial) full-face view. B) lateral view of the body. C) mandibular setae. and, D) close-up of mandible setae.

Figure 2. *Tatuidris tatusia* type series, showing pilosity pattern A. A-D) Full face view, lateral view, dorsal view, and label of *T. tatusia* Holotype. E-G) Full face view, lateral view, dorsal view, and label of *T. tatusia* Paratype (MCZ collection Type locality: El Salvador [Brown and Kempf 1968]).

Figure 3. Images of *Tatuidris tatusia* gyne. A) Dorsal view. B) Head in full face view. C) Detail of the wings; and, D) Lateral view of the body.

Figure 4. Images of *Tatuidris tatusia* male. A) Dorsal view. B) Head in full face view. C) Detail of the wings; and, D) Lateral view of the body.

Figure 5. *Tatuidris tatusia* and specimens showing pilosity pattern A. A-C) Full face, lateral and dorsal view of *T. tatusia* from Matagalpa, Nicaragua. D-F) Full face, lateral and dorsal view of *T. tatusia* from Otongachi, Ecuador. G-I) Full face, lateral and dorsal view of *T. tatusia* from Maquipucuna, Ecuador. J-L) Full face, lateral and dorsal view of *T. tatusia* from Cuzco, Peru.

Figure 6. *Tatuidris tatusia.* Specimens showing pilosity pattern B. A-C) Full face, lateral and dorsal view of *T. tatusia* from Caves Branch, Belize. D-F) Full face, lateral and dorsal view of *T. tatusia* from Belmopan, Belize. G-I) Full face, lateral and dorsal view of *T. tatusia* from Maquipucuna, Ecuador.

Figure 7. *Tatuidris tatusia.* Specimens showing pilosity pattern C. A) Full face and B) lateral view of *T. tatusia* from Puntarenas, Costa Rica.

Figure 8. *Tatuidris tatusia.* Specimens showing pilosity pattern D. A-C) Full face, lateral and dorsal view of *T. tatusia* from Los Tuxtlas, Mexico D-F) Full face, lateral and dorsal view of *T. tatusia* from Chiapas, Mexico. G-I) Full face, lateral and dorsal view of *T. tatusia* from Magdalena, Colombia.

Figure 9. Visual representation of *Tatuidris* pilosity patterns.

Figure 10. Neighbor joining tree based on K2P distances for 28 *Tatuidris* specimens and four other ant taxa as outgroups. Labels consist of countries, first division, localities, and specimen IDs. Specimens with pilosity pattern "D" are highlighted in yellow. Specimens with pilosity pattern "B" are highlighted in light blue. Specimens with no color present a pilosity pattern "A", similar to the type series. Asterisks above nodes represent nodes with >50% bootstrap support (999 repetitions). The tree is drawn to

scale, with branch lengths in the same units as those of the evolutionary distances used to infer the phylogenetic tree.

Figure 11. Linear regression between genetic distance (pairwise divergence) and geographic distance.

Figure 12. PC scores for specimens included in this analysis. Symbols represent different pilosity patterns. Circles = pilosity patter A (similar to type series). Crosses = pilosity patter B. Triangles = pilosity patter C. Xs = pilosity patter D.

Figure 13. Map of localities of specimens included in this study. Black diamonds represent localities from which specimens included in the COI DNA barcodes analysis were obtained. Circled stars represent type localities from the two previously know species (e.g. *Tatuidris tatusia* Brown and Kempf, and *Tatuidris kapasi* Lacau and Groc syn. nov.).

Figure 14. Lateral-diagonal view of head of *Phalacromyrmex* sp., from Brazil, showing position of antennal sockets on head capsule. In *Phalacromyrmex*, the antennal socket is located up-side down in a way similar to that of *Tatuidris*. Photo courtesy of R. Feitosa.

Figure 1. Chapter 3

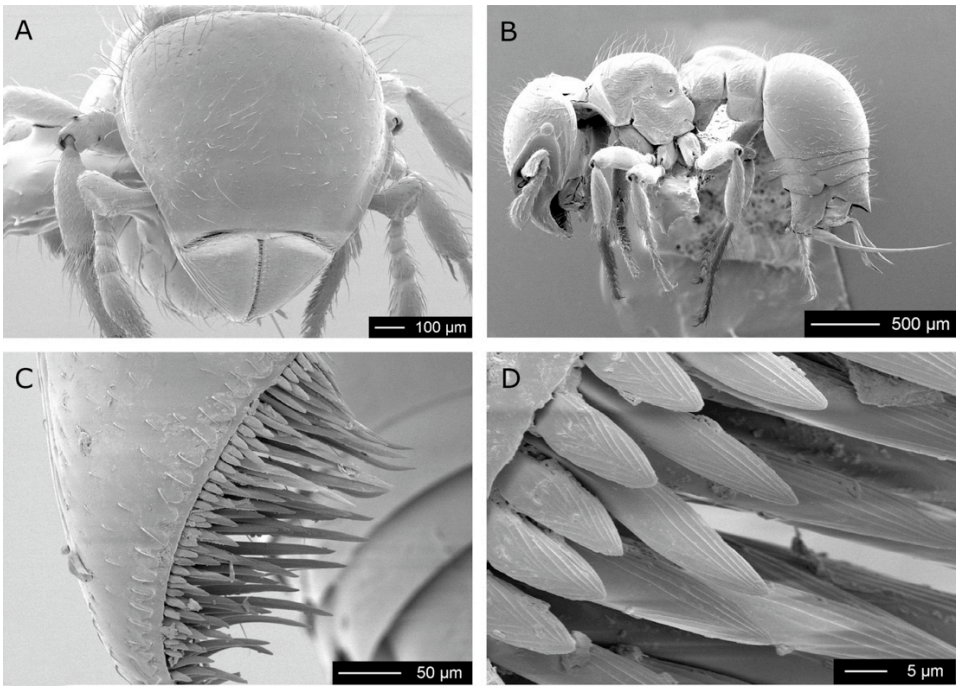


Figure 2. Chapter 3

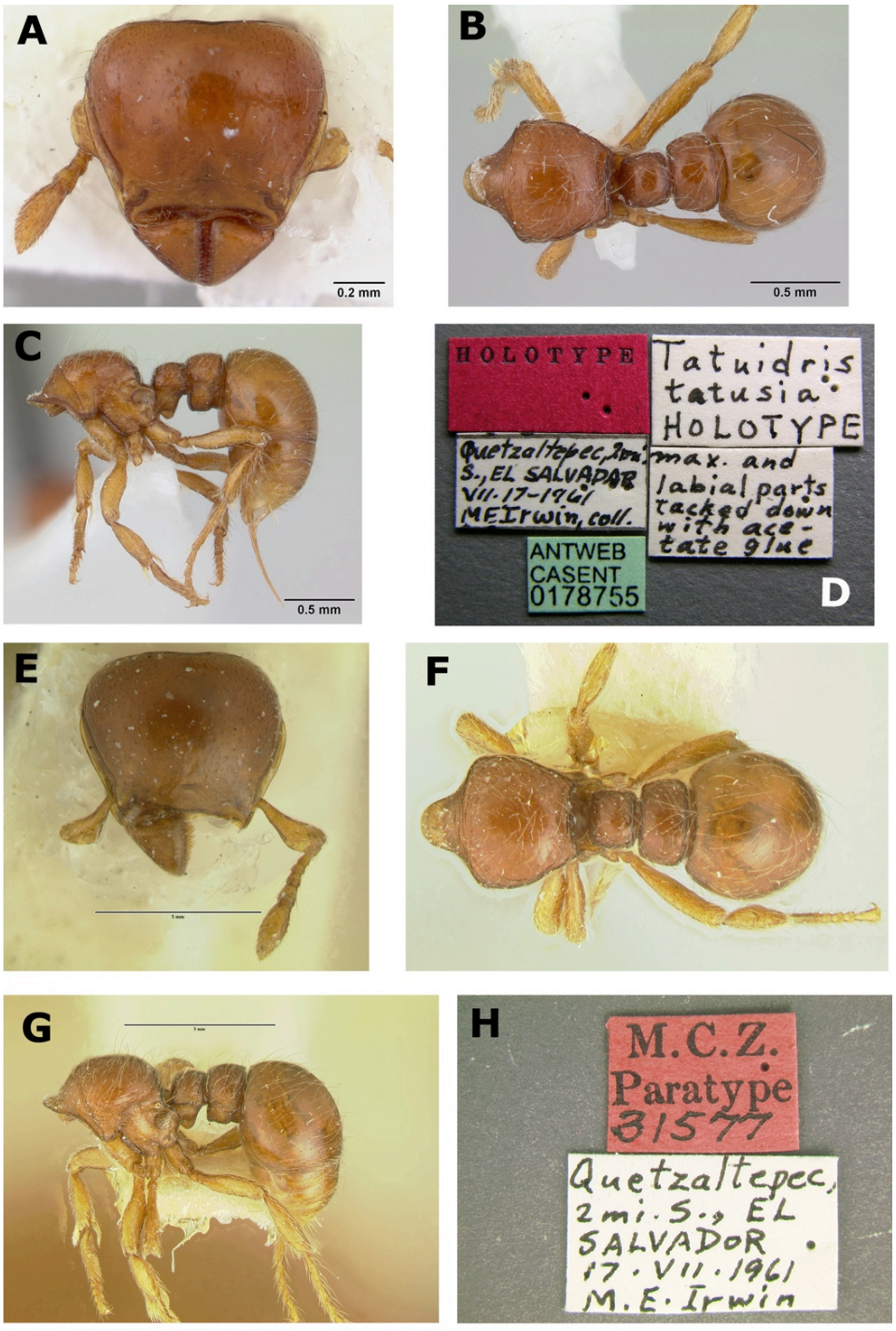
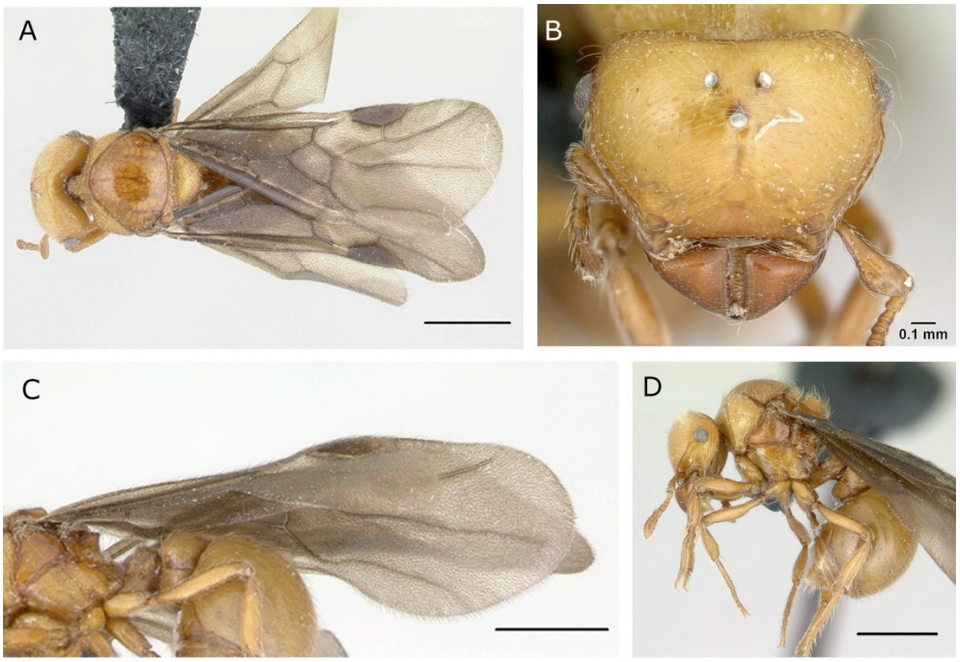


Figure 3. Chapter 3



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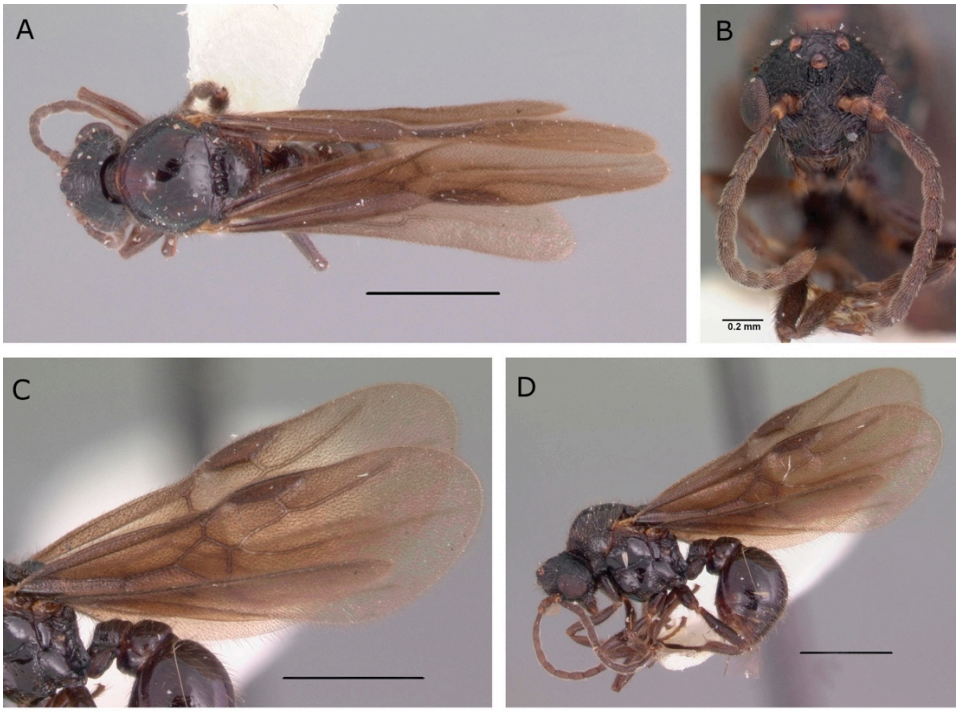

Figure 5. Chapter 3

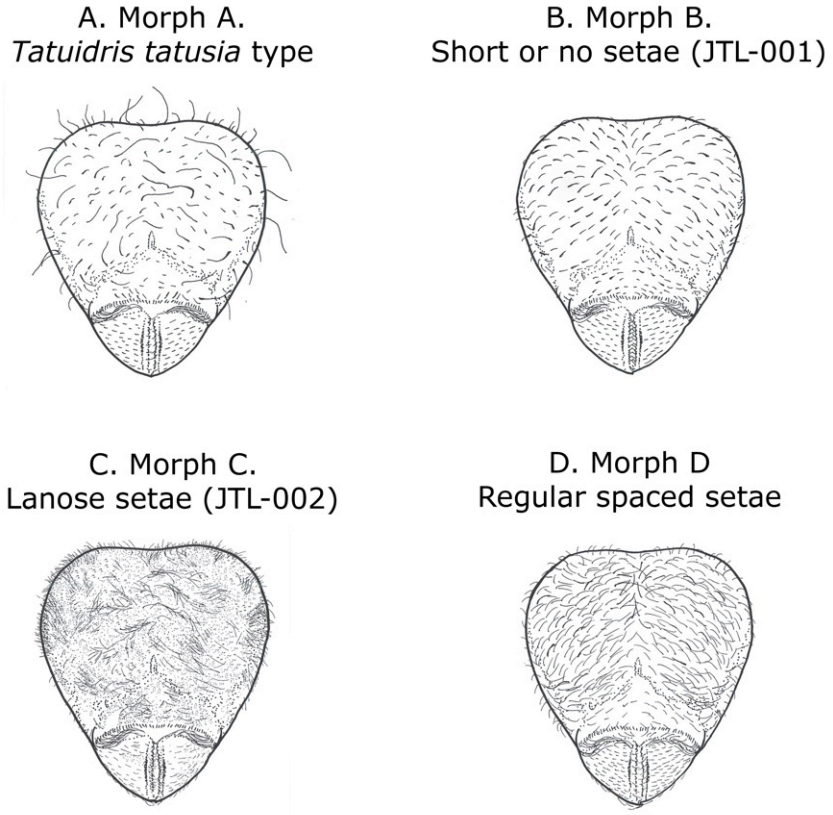

Figure 6. Chapter 3

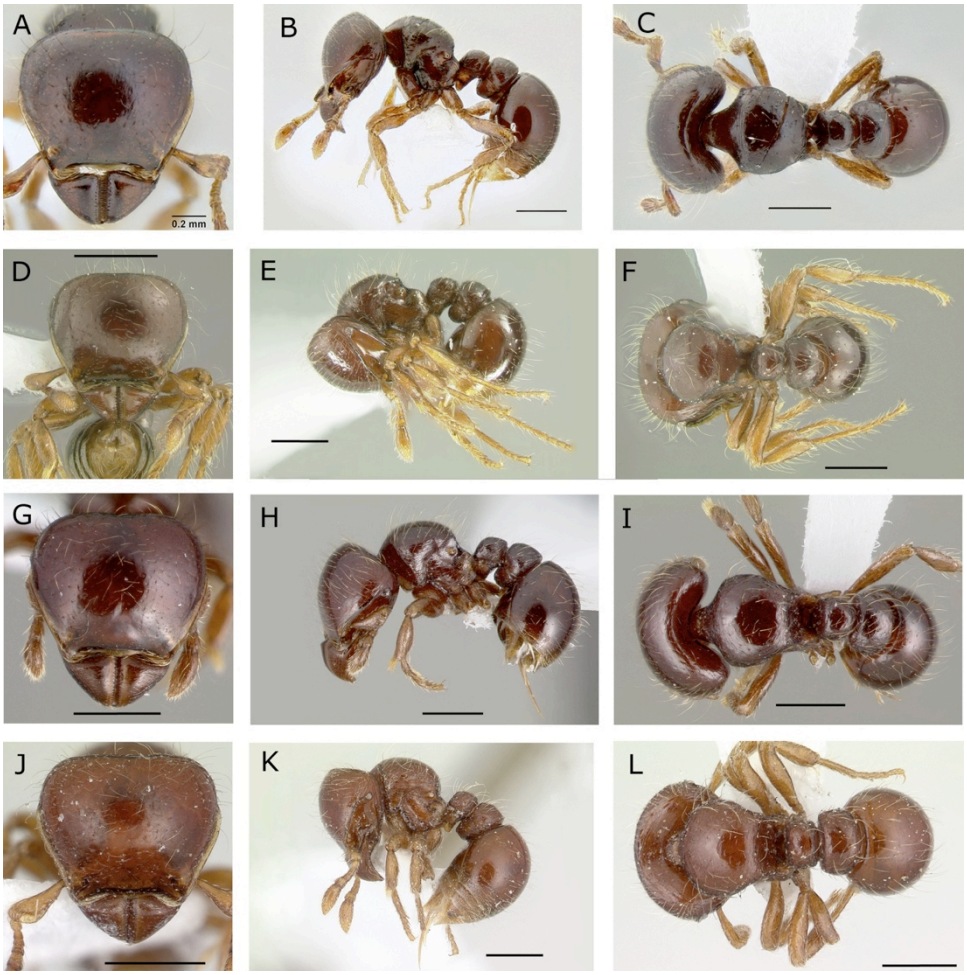

Figure 7. Chapter 3

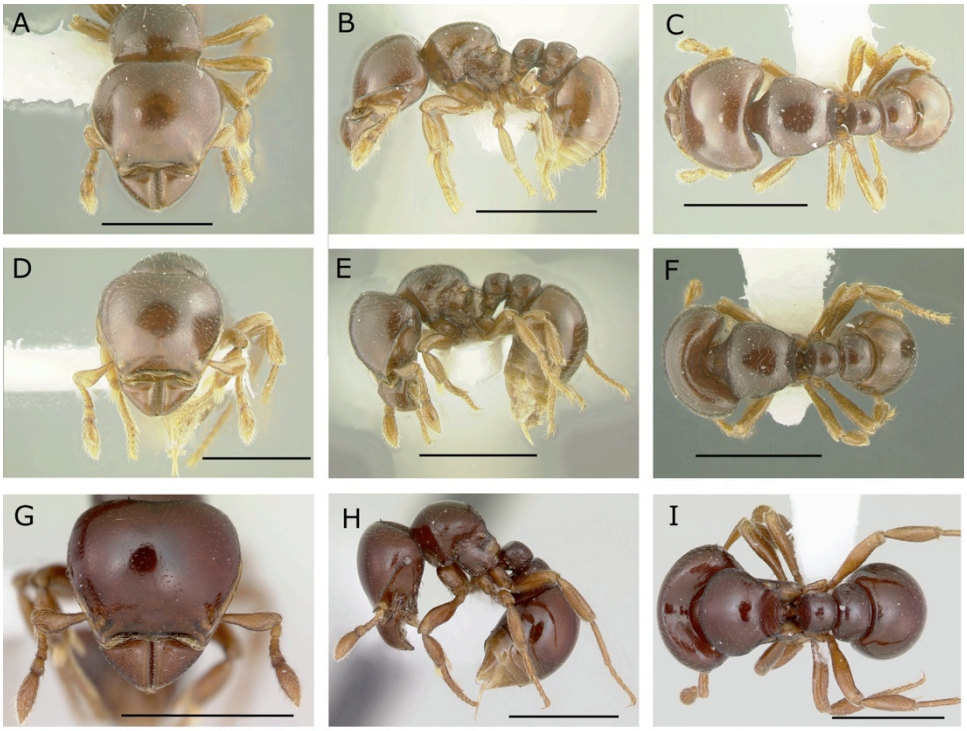

Figure 8. Chapter 3

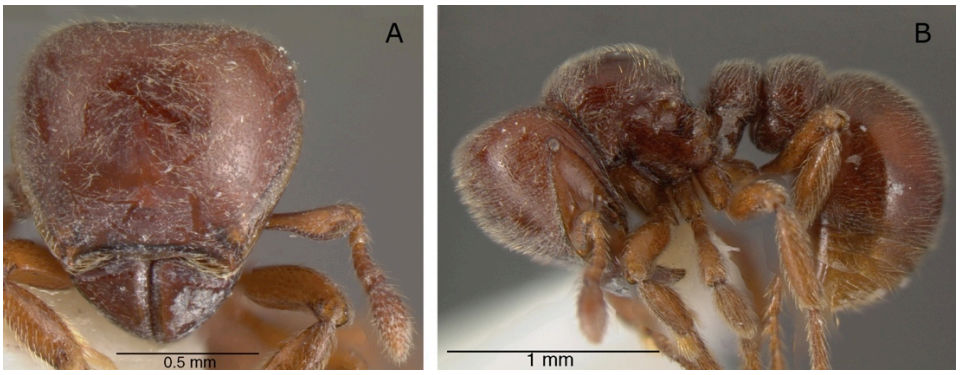

Figure 9. Chapter 3

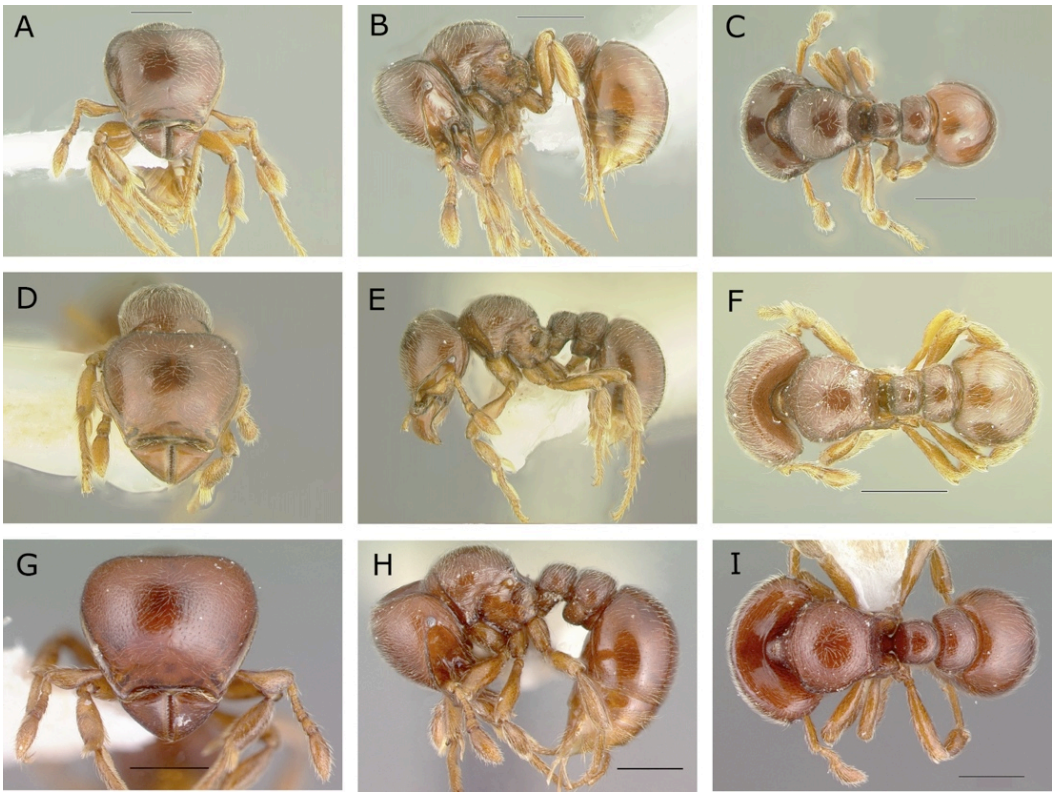

Figure 10. Chapter 3

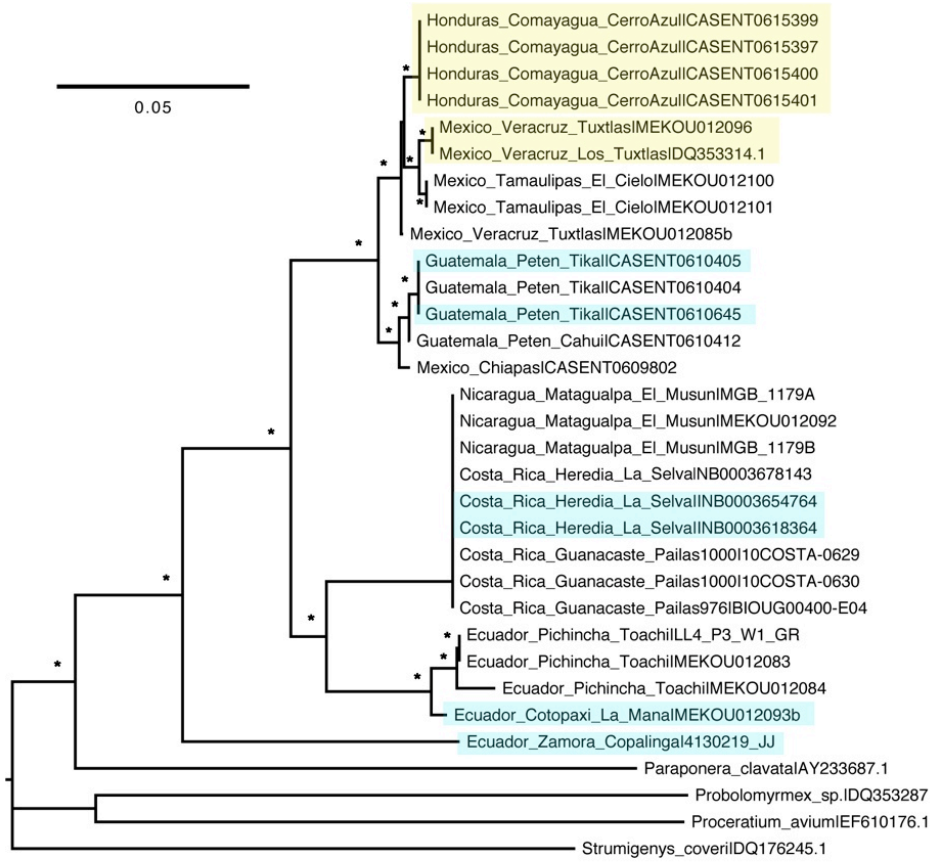

Figure 11. Chapter 3

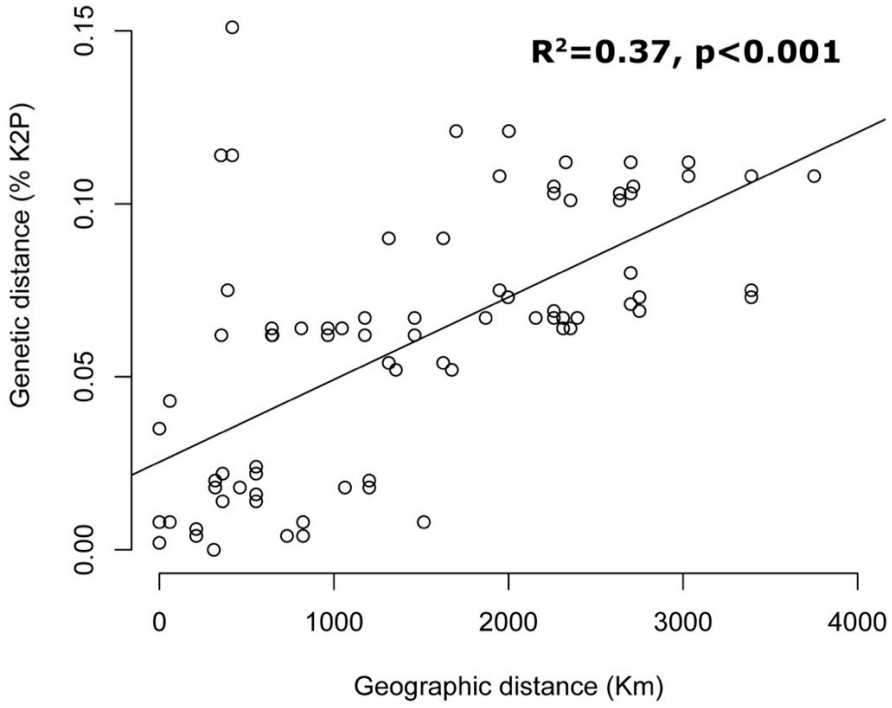

Figure 12. Chapter 3

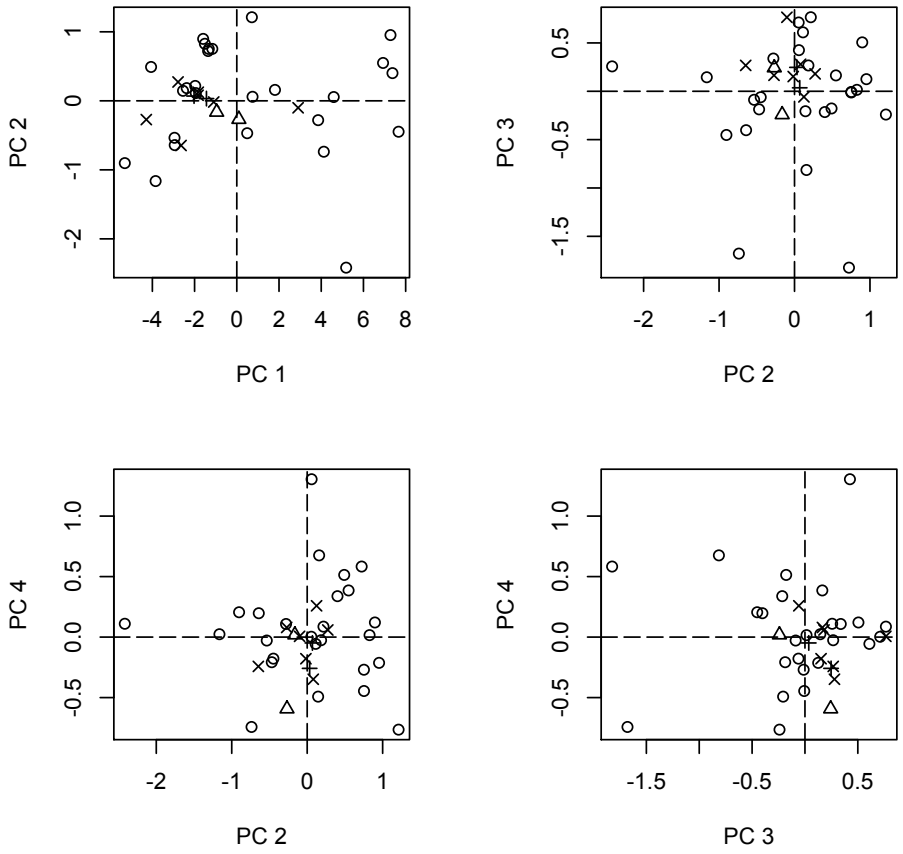

Figure 13. Chapter 3

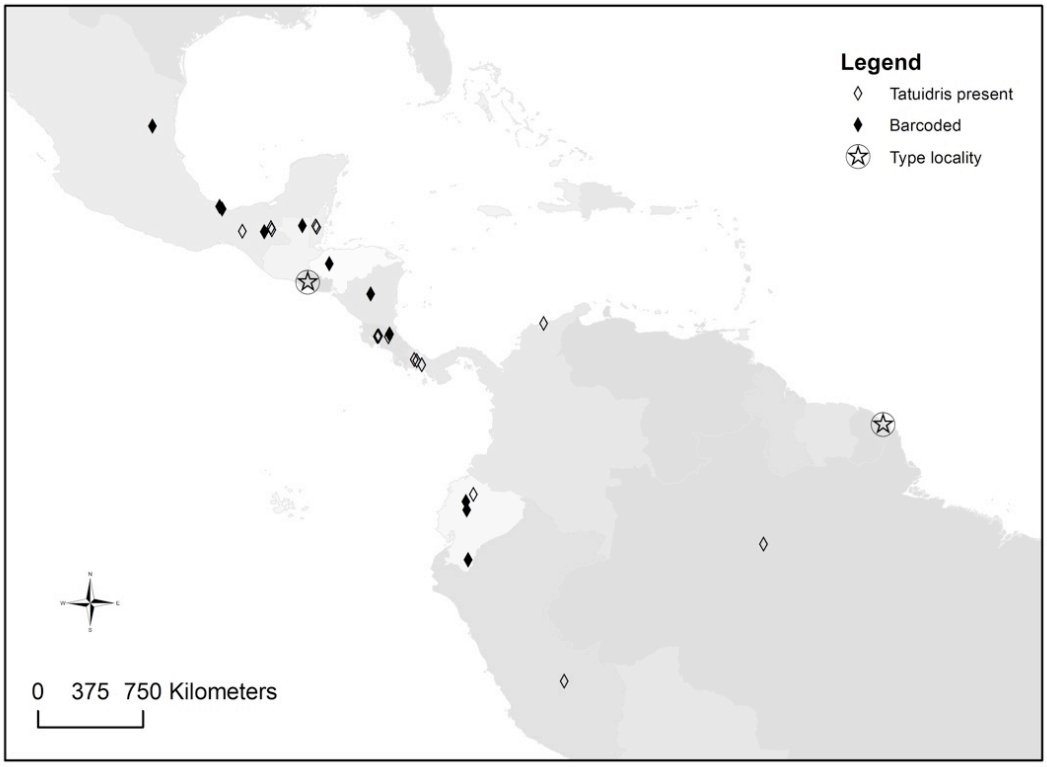

Figure 14. Chapter 3

CHAPTER 4: PREDATION BY LITTER ANTS IN A BROWN FOOD WEB: DIMINISHING EFFECTS FROM MICROBIVORY TO DECOMPOSITION RATES

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Abstract

1. Ants are conspicuous predators within tropical brown food webs, but their trophic interactions with other litter invertebrates and impacts on nutrient cycling remain little understood.
2. In a two-month field experiment, we used a sucrose supplementation assay to increase litter ant abundance. Then, we tested the general hypothesis that ants reduce the numbers of litter predators, shredders, and microbial grazers, and ultimately, shape rates of litter decomposition.
3. After one month, ant abundance increased in sucrose plots. This increase was accompanied by significant reductions in two shredder taxa, Gastropoda and Isopoda. Among predator taxa, only Trombidid mites responded, with decreases in abundance.
4. After two months, the native form of the invasive ant *Wasmannia auropunctata* came to dominate sucrose plots, decreasing the overall abundance of other ants, shredders (Hemiptera). Predator responses in sucrose plots were more variable at this time, with counts of Aranea decreasing, and counts of Trombidiidae increasing. During the length of this experiment, there was no evidence of changes in litter depth or rates of decomposition.
5. Structural analysis of food webs gave stronger support to a top down model of BFW organization, but one that attenuated at the links between shredder/grazers and the microbe/litter environment.
6. Our study highlights the importance of temporal scales in the study of trophic interactions among tropical litter taxa. We conclude that effects of predation by

litter ants in other litter taxa is limited by nutrient availability and molded by growth-defense tradeoffs among detritivore taxa.

Key-words: Formicidae, *Wasmannia auropunctata*, top-down control, bottom-up regulation, tropical forests.

Introduction

About 90% of terrestrial production enters the detrital or "brown" food web (BFW) comprised of decomposer bacteria, fungi, and invertebrates (Swift, Heal and Andersen 1979). Hairston, Smith and Slobodkin (1960; HSS) in their first synthesis on trophic regulation conclude that decomposers "as a group must be food limited"; shifting the search for predator effects on food webs to the green food webs of plants, herbivores, and their predators (Power 1992, Moore *et al.* 2004, Coleman 2007). The trophic ecology of BFWs, however, is of considerable interest. They are half of the biotic part of the carbon cycle (Hattenschwiler and Gasser 2005), they are patchy in space and time at multiple scales (Berg and Bengtsson 2007), and the rapid dynamics driven by their small sizes allow one to study multiple generations over a relatively short time (Wardle and Yeates 1993, Scheu and Setälä 2002).

Predators perform important roles within food webs, exerting top-down control on community structure, and serving as food for other predators and parasites (Schmitz, Hambäck and Beckerman 2010, Terborgh and Estes 2010, Estes *et al.* 2011). Ants, well-known top predators in litter environments, are a species- and functional-rich component of tropical forest, accumulating up to 30% of total tropical animal biomass (Fittkau and Klinge 1973). Ant-prey interactions are widespread, and ants are known to feed upon many arthropod groups (Kaspari *et al.* 2011). Ant-predator interactions are also varied, including intraguild predation and interference competition (Moya-Laraño and Wise 2007, Sanders and Platner 2007). Moreover, ants can positively affect abundances of other BFW taxa, if these taxa benefit from ant nest-effects (Schuch, Platner and Sanders 2008) and mutualistic relationships (Henderickx 2011). Effects of

ants on abundances of some arthropod taxa can also be minimal. For example, experimental exclusion of a dominant dolichoderine ant species in Australian rock outcrops did not translate into changes of biomass or abundance of other arthropod taxa (Gibb 2003). While many ecological interactions between ant and other arthropod taxa are know to exists, much is still unknown about the number and strength of trophic interactions that ants can exert in BFWs, which is particularly true for tropical ecosystems.

Beyond trophic levels, there may be considerable variation in the susceptibility of prey taxa to predators if defenses are not uniformly distributed throughout food webs (Coley and Barone 1996, Schmitz, Hambäck and Beckerman 2000). Scheu and Setälä (2002) argue that the ubiquity of defenses among consumers in BFWs limits the impacts of predators on prey; impacts that may reflect tradeoffs between chemical defenses and growth rate (Kaspari and Yanoviak 2009). For example, chemical defenses –alkaloids, p-benzoquinones, phenols, cyanogens, and quinazolinones– are plentiful between two common litter invertebrate taxa: oribatids and diplopods (Eisner *et al.* 1978, Saporito *et al.* 2007). In a comparative study looking at the geography of tropical BFWs, Kaspari and Yanoviak (2009) found that these defended invertebrates increased at the expense of more palatable isopods and collembolans when ant densities were high. We thus hypothesize that within our study site (i.e. the litter layer of a single forest stand with fertile shallow soils) increasing predator pressure should favor the consumption of fast growing and relatively undefended collembolans and isopods over the more chemically protected oribatids and diplopods (Endara and Coley 2010).

Less is known, however, about the consequences for trophic control of the microbes and detritus that grazers and shredders in a BFW eat. For decades, the HSS view of weak top down regulation of BFWs persists given the chemical defenses of fungi and diversity of omnivory (Mikola and Setälä 1998, Scheu and Setälä 2002), even when trophic cascades within soil ecosystems have long been recognized (Santos, Phillips and Whitford 1981, Lensing and Wise 2006); and examples of ants as main drivers of trophic cascades and nutrient cycling exists (O'Dowd, Green and Lake 2003, Zelikova, Sanders and Dunn 2011). Similarly, in a review of green food webs, suggested that top-down effects should attenuate as diversity increases and defenses proliferate at lower trophic levels. But factors such as rain (Lensing and Wise 2006) and microbial energy channels (Wardle and Yeates 1993) can contribute to variability in top-down control across ecosystems (Wardle 2010). Recent syntheses suggest that the paradigm of bottom-up regulation of BFWs arises in part from a shortage of experiments and poor comprehension of the many different roles that predators can play in a complex food webs (Schmitz 2010, Power 1992), which is particularly true for tropical ecosystems.

We used a food supplementation experiment to explore the predatory-driven consequences of increasing ant abundance on BFW structure and litter breakdown. By directly manipulating sucrose availability, we attracted ants to treatment plots without otherwise supplementing them with habitat resources, which are known to affect BFW structure (Doblas-Miranda *et al.* 2009; Shik and Kaspari 2010; Lessard *et al.* 2010, Wilder et al. 2011). We explored the ability of ants to regulate directly the abundance of 14 other taxa (grouped as predators, microbial grazers, and litter shredders); and

indirectly, microbial decomposition and litter depth. We further tested the general hypothesis that distribution of chemical defenses among prey taxa can explain in part predation rates as predation pressure increases. Finally, we evaluated two models (top-down vs. bottom-up) of trophic control of BFWs by testing the correlation of abundance among functional groups. In the process, we gained insight as to what happens when one inadvertently promotes the domination of the litter substrate by an invasive ant in its own habitat.

Materials and Methods

This experiment was performed over the course of two months from June 01 to 31 August 31, 2009, on Barro Colorado Island (BCI; 09° 09′ N, 79° 51′ W), a seasonal tropical forest managed by the Smithsonian Tropical Research Institute in Panama. BCI receives ca. 2600 mm of annual rainfall, with nearly 90% falling from May to December (Leigh *et al*. 1999). Sampling thus occurred from early to mid wet season on BCI —a period of high ant activity (Levings 1983, Kaspari, 1996b).

Manipulating resource availability

Food press experiments were performed at one site (trail mark: Barbour 9) on BCI. In this site, 30 3x3-m blocks, each with one control and one food addition 0.25-m^2 paired plot, were arrayed in a 3x10 grid. The blocks within the grid were separated by 5 m on each side. Treatments were randomly assigned to plots and consisted of 10% (w/v) sucrose food (+CHO) and water (Control). Sucrose was presented as agars (80 mg/ml). On each plot, we placed 1.2 g pieces of each food on separate 2 cm^2

notecards. Notecards were monitored for ant activity and when necessary non-ant arthropods were not allowed to harvest food. We retired the notecards after 1h.

Measuring invertebrate responses

After 30 days (Month 1) we harvested 20 randomly selected blocks; the remaining 10 blocks were harvested after 60 days (Month 2). Litter in each plot was collected down to mineral soil and placed in a large plastic bag. In the lab, we searched for and removed litter ant nests. Then we extracted the remaining invertebrates by sifting the litter vigorously through 1 cm mesh and running the residuals through a Berlese funnel for 48 h (Bestelmeyer *et al.* 2000). We quantified the abundance (individuals $0.25m^{-2}$) of 15 invertebrate taxa from three functional groups based on the literature (Swift, Heal and Andersen 1979, Coleman, Crossley and Hendrix 2004, Kaspari and Yanoviak 2009).

Predators included ants (Formicidae), three mite taxa (Acari: Mesostigmata, Prostigmata and Trombidiidea), spiders (Araneae), opilionids (Opiliones) and Pseudoscorpions (Pseudoscorpionida). Microbial grazers (henceforth grazers) included collembolans (Collembola), maggots (Diptera larvae), hemipterans (Hemiptera), thrips (Thysanoptera) and Oribatid mites. Shredders (or comminuters) included isopods (Isopoda), diplopods (Diplopoda), and gastropods (Gastropoda). During the experiment, we noticed that the invasive ant *Wasmannia auropunctata* (Roger 1863), albeit, in its native range (Wetterer and Porter 2003) came to dominate in sucrose plots, we thus decided to run the analysis on ants using 1) total ant counts, 2) total ant counts minus *W. auropunctata*, and 3) W. auropunctata alone.

We used a Negative Binomial GLM (i.e. an 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 on +CHO vs. Control plots. Negative Binomial GLMs are designed to fit data that lacks normality, as it is generally the case for counts of invertebrate taxa across sampling points (Sileshi 2006). Fitting our invertebrate counts to Negative Binomial models usually provided a better fit than the regular Poisson model did; however, an extensive set of comparisons between the two models suggested that the Negative Binomial were more sensitive to these extreme, but rarer, counts that are less likely to represent responses to our treatments (e.g. catches of large ant colonies, or collembolan and oribatids blooms). We used a Pearson Chi-Square test (X^2) to test the general hypothesis that our experimental treatments have a significant explanatory power. We used R v.2.13.1 (R Development Core Team, 2006) using the "MASS" (Venables and Ripley, 2002) and "lmtest" (Zeileis and Hothorn 2002) packages.

Measuring decomposition rates and changes in litter depth

At the outset, each plot was seeded with litterbags (0.02mm nylon mesh bottoms and 3 mm nylon mesh tops) stocked with two pieces of filter paper, qualitative grade, and a pine "popsicle" stick). Both substrates were pre-weighed at 1.3-1.5g. These were slipped below the litter at the soil surface and harvested with the litter after one or two months. The filter paper and sticks were rinsed clean and dried to constant mass at 40°C. Decomposition rates were estimated as percent dry mass loss. At harvest we also measured litter depth (cm), as a metric of standing crop. At four corners of each plot,

we inserted a metal wire through the litter until it reached mineral soil, and used a ruler to measure the displacement. We compared litter depth and decomposition rates across the two treatments using a Wilcoxon Signed rank test.

Synthesis: comparing top-down vs., bottom-up models of organization

We used structural analysis (Mitchell 1992) using the SAS 9.1 Proc Calis (SAS 2006) to evaluate the comparative fit of top-down and bottom up models of food web organization, as revealed by our experiment. Structural analysis uses maximum likelihood estimation to generate standardized coefficients that describe the relative magnitude of the proposed trophic linkages between ants, other predators, grazers, shredders, average decomposition rate (the mean percent loss of both substrates month^{-1}), and litter depth. Bentler's comparative fit index (0-1) assesses the overall fit of the data to the model, with values over 0.9 indicating a good fit.

Results

Ant abundance

Ant abundance had a variable response in +CHO plots across months (Table 1, Fig. 1). At Month 1, ant abundance had increased by 72% on +CHO plots ($X^2 = 5.09$, $p < 0.024$); by Month 2 however, this difference had disappeared ($X^2 < 0.001$, $p = 0.947$) (Table 1). Changes in ant community composition could explain in part these results and, on closer inspection of the data, the increase in total ant abundance was driven by *Wasmannia auropunctata,* the most common ant species in this habitat. For example, *W. auropunctata* was in Month 1 five times as common on +CHO plots ($X^2 = 4.36$, $p <$

0.037), and, in Month 2, two times more abundant ($X^2 = 1.49$, $p < 0.222$). However, this relationship was driven by a extreme value (likely, counts of a complete colony in one Control plot). When removing this data point, ants in Month 2 were 18 times more abundant in +CHO plots ($X^2=10.15$, $p<0.001$). On the other side, when all other ant species (i.e. except *W. auropunctata*) were tallied, ant abundance increased on average in Month 1 by 39% but had actually decreased some 23% in Month 2.

Invertebrate responses

In Month 1, the abundance of two of the three shredders (but of no grazer) had responded to +CHO treatments. As predicted, increasing ant abundance favored two defended taxa—oribatids and diplopods that decreased by 26.8% and 28.5%, respectively, but not in significant ways (Oribatida, $X^2 = 1.71$, $p < 0.19$) (Diplopoda, $X^2 = 0.58$, $p < 0.446$). They did so at the expense of less defended taxa—isopods (-60 %), maggots (-8.4%) and gastropods (-55.2%), although only gastropods and isopods showed a significant trend ($X^2 = 5.03$, $p < 0.025$; $X^2 = 3.94$, $p < 0.047$; respectively). Of the six other predatory taxa, Trombidoidea mites responded with a reduction of 70.4% ($X^2 = 5.93$, $p < 0.015$).

By Month 2, when *W. auropunctata* came to dominate in +CHO plots, collembolans hemipterans ($X^2 = 9.08$, $p < 0.003$) decreased. Diplopods, isopods and gastropods, in contrast were unchanged. Likewise, predators began to show changes in abundance. Spiders and pseudoscorpions that trended higher in Month 1, by Month 2 they declined by 40.7% and 37.8%, respectively, albeit non significantly (Spiders, $X^2 = 3.09$, $p < 0.079$, Pseudoscorpionida, $X^2 = 1.00$, $p < 0.318$).

Decomposition rates and litter depth

Decomposition rates did not vary with +CHO treatment. Filter paper showed an average loss mass change of -1.1% and +2.3% on +CHO plots in Month 1 and Month 2, respectively (Month 1, Wilcoxon $U_{=}$ 110, p = 0.56; Month 2, Wilcoxon $U_{=}$ 22, p = 0.57). Wooden sticks showed an average mass loss of 22.6%, and 22.5% on +CHO plots in Month 1 and Month 2, respectively (Month 1, Wilcoxon U = 101, p = 0.43; Month 2, Wilcoxon U = 26, p = 0.72).

Litter depth, too, was invariant across the two treatments. Litter increased by 8.7% in Month 1 in +CHO plots (Wilcoxon U = 72, p = 0.82). In Month 2, litter decreased by 1.2% in +CHO plots (Wilcoxon U = 25, p = 0.59).

Synthesis: top down vs. bottom up models of organization

Structural analyses yielded standardized coefficients with higher overall fits to the top down model (Fig. 2). Bentler's comparative fit index was higher for month 1 (B = 0.85) and month 2 (B = 0.77) for the top down model of ant control of predator, grazer and shredder abundance, than for a model of litter and decomposition control (B's == 0.69 and 0.62). Moreover, in both cases, the standardized coefficients linking decomposition litter depth to grazers and shredders were uniformly low (0-0.3) while the magnitude of ant effects on grazers, shredders, and other predators were generally much higher. In the top down model, increasing ant abundance on plots was

accompanied by increases in other predators, and decreases in grazers and shredders, although this, in turn, showed little effect on decomposition rates or litter depth.

Discussion

Five decades after HHS, the relative strength on top-down forces, versus bottom-up regulation in shaping litter communities remain unassessed. Here, by feeding ants with sucrose we significantly increased their abundance in treatment plots, especially that of *Wasmannia auropunctata*, and reduced densities of several grazer and detritivore arthropod groups such as isopods, hemipterans and gastropods. However, these changes in prey abundance did not propagate further in the food web and, e.g. both litter depth and decomposition rates did not respond to our treatments; and variable through time. This lack of top-down effects in our tropical BFWs is unexpected but not surprising. Previous research suggest that trophic cascades are likely attenuated in highly diverse communities, where omnivory is the rule, and species at lower trophic levels have chemical defenses (Schmitz, Hambäck and Beckerman 2000, Polis 1991, Wardle and Yeates 1993, Polis and Strong 1996, Sheu and Setala 2002, but see O'Dowd, Green and Lake 2003). Experiments thus remain a key method to contrast resource (bottom-up) and predator (top-down) control of BFWs, and the ecological pressure that predators exert in tropical BFWs and nutrient cycling (Sih *et al.* 1985, Lawrence and Wise 2000).

The marginal increases of prostigmatid and trombiidids mites (e.g. among the top predators of BFWs) in our experiment suggest instead that bottom-up resource limitation is widespread in our system. Evidence for bottom-up resource limitation and

attenuating effects up in the trophic food web have arisen by experiments supplementing BFWs with chemical nutrients (Scheu and Schaefer 1998, Chen and Wise 1999, Lessard *et al.* 2010, Shik and Kaspari 2010) or added leaf litter directly to plots (Sayer, Tanner and Lacey 2006, Oelbermann, Langel and Scheu 2008). Most of these studies have found positive responses of detritivore taxa and their predators to the treatments, usually associated to increases in decomposition rates (Chen and Wise 1999, Milton and Kaspari 2007, Shik and Kaspari 2010). At least one study (Milton and Kaspari 2007) suggested absorption of microbivore numbers through predator recruitment. However, resource supplementation via litter additions in BFWs confounds added habitat availability and food availability (Shik and Kaspari 2010). Indeed, when Oelbermann *et al* (2008) added *Drosophila* to plots in their grassland experiment, they found no evidence of increasing invertebrate number. And, litter depth alone can explain increases in predator taxa (Donoso *et al.* unpublished). Our experimental design allowed us to separate these effects by providing nutrients, but not habitat, to litter communities. Thus, increases in trombidids and prostigmatids mites, parasites and predators of a wide variety of arthropods and vertebrates (Uppstrom and Klompen 2011, Henderickx 2011), supports a plausible working hypothesis that the loose unicolonial nests of *W. auropunctata* provide food and/or shelter for these mite taxa (Wetterer and Porter 2003).

A major paradigm of green food webs is that plant defenses abound in slow growing plant species, because of relatively high costs that herbivores would imprint on them (Coley, Bryant and Chapin 1985, Endara and Coley 2010). Our study suggest that grazers and shredders at the base of BFWs can behave similarly to plants and that their

chemical defenses, known to be related to their growth rates (Kaspari and Yanoviak 2010), may have an impact in the rate of predation they support. For example, both diplopods and oribatids, which are relatively well-defended taxa, remained unaffected since the start of the experiment. We suggest that the inability of ants to regulate diplopod and oribatid abundance, even when evidence suggest that these taxa is in the ant's diet (Wilson 2005), could be attributable to ants feeding on fast-growing, less-defended taxa such as collembolans and isopods. In fact, the lack of an effect on the abundance of both collembolans (see also Zelikova *et al.* 2011) may be a result of their high turnover rate. Clearly, differential predation among soil taxa by their predators may explain in part the chemical constituency of their bodies.

The invasive ant *Wasmannia auropunctata* have been implicated in the local depletion of native ant species and selected arthropods (Wetterer and Porter 2003, Walker 2006), although such effects have been correlational and/or anecdotal. Our results, and similar food supplementation experiments with insect protein (Shik and Kaspari 2010), suggest that *W. auropunctata* have the ability to recruit to and dominate localized food sources in their native habitat (McGlynn 2006, Shik and Kaspari 2010). But, specific mechanisms for *Wasmannia* dominance in litter environments remain elusive. Orivel *et al.* (2009) suggest *W. auropunctata* populations are larger and more aggressive in species poor, anthropogenically disturbed habitats (made up 3% of baits in primary forest, and 41% of open habitats in French Guiana). Our experimental grid, located in an old second growth forest, matched their open forest scenario, where *W. auropunctata* occurred in 50% of all berlese samples. This lead us to suggest that responses of the arthropods included in this study were due in part to the ability of *W.*

auropunctata to monopolize sugar baits.

Figure Legends. Chapter 4

Figure 1. Box plots representing effects of +H20 and +CHO baits on the abundance of litter invertebrates after "1" and "2" months. Invertebrates are grouped into four functional groups: ants, other predators, shredders and microbial grazers. Stars represent significant differences of among treatments. Star within parenthesis highlight non-significant trends.

Figure 2. Structural analyses evaluating two hypotheses of food web organization over the first and second month of the experiment. Taxa/rates at the end of a line with a circle are posited to be inhibited by the other taxa/rate; those at the end of a line with an arrow are posited to be promoted by other. B is the Bentler's comparative fit index; values associated with arrows are the standardized coefficients.

Figure 1.

Chapter 4

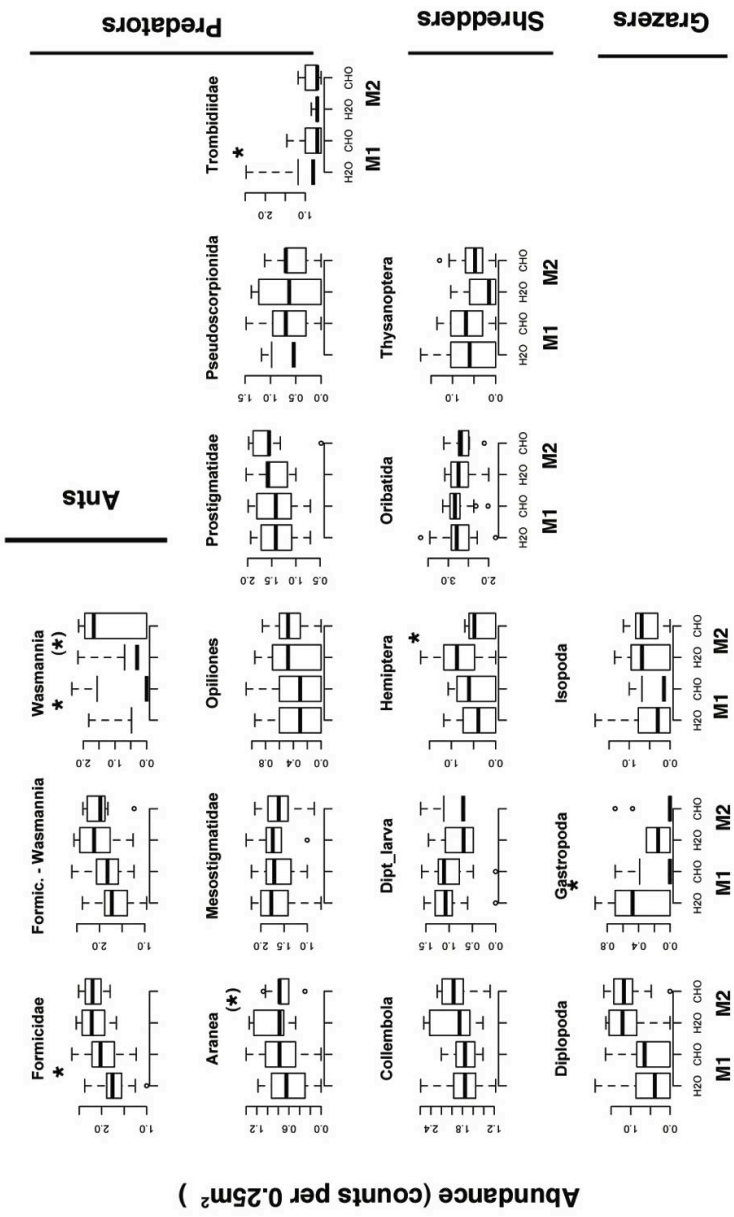

Figure 2. Chapter 4

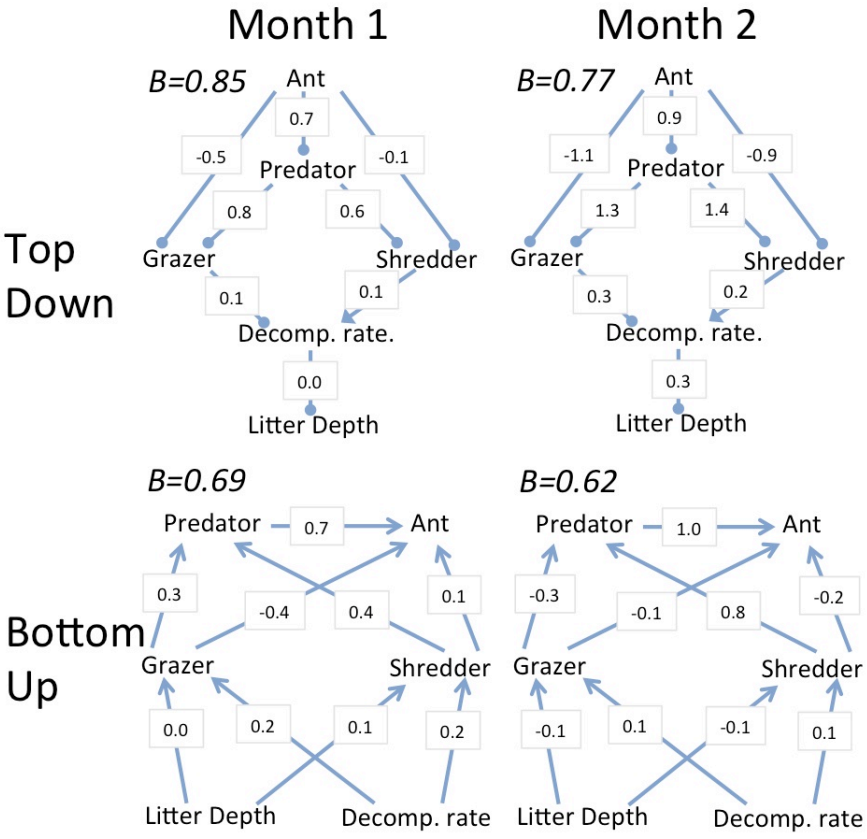

Table Legend. Chapter 4.

Table 1. Abundance of invertebrate taxa (mean no. individuals/0.25m^2) in response to food addition (+H_2O vs. +CHO) after one and two months. P values generated by Negative Binomial GLM (X^2); we highlight in bold the plot with higher abundance significant at $p<0.05$. Results from our decomposition experiment and changes in litter depth are given at the bottom.

Table 1. Chapter 4.

	Month 1						
	+H2O	+CHO	%	Est.	Dev	X2	P
Formicidae	74.6	128.5	72.2	0.54	43.2	5.09	0.024
F-W	70.0	97.6	39.4	0.33	43.6	1.72	0.190
Wasmannia	4.8	31.0	545.8	1.87	35.7	4.36	0.037
PREDATOR							
Aranea	5.7	7.7	35.9	0.31	44.3	1.44	0.230
Mesostigmatidae	63.7	57.8	-9.1	-0.10	45.7	0.12	0.726
Opiliones	2.8	2.7	-3.5	-0.04	42.6	0.01	0.903
Prostigmatidae	34.8	35.9	3.0	0.03	48.7	0.01	0.932
Pseudoscorpionida	5.0	6.7	32.6	0.28	45.7	0.79	0.373
Trombidoidea	24.1	7.1	-70.3	-1.22	46.4	5.93	0.015
GRAZER							
Collembola	86.5	65.6	-24.2	-0.28	42.4	1.70	0.193
Dipt_Larva	14.3	13.1	-8.3	-0.09	42.7	0.16	0.686
Hemiptera	3.8	4.5	18.1	0.17	42.1	0.33	0.563
Oribatida	917.2	670.9	-26.8	-0.31	43.5	1.71	0.191
Thysanoptera	7.9	7.1	-10.1	-0.11	45.4	0.09	0.770
SHREDDER							
Diplopoda	11.0	7.9	-28.5	-0.34	45.3	0.58	0.446
Gastropoda	2.9	1.3	-55.1	-0.80	45.6	5.03	0.025
Isopoda	7.3	2.9	-60.5	-0.93	43.4	3.94	0.047
BIOMASS	Control	+CHO	%			V	P
Litter depth	3.0	3.3	8.7			72	0.820
Decomp.Filter	26.4	26.1	-1.1			110	0.560
Decomp.Popsicle	12.4	15.2	22.5			101	0.430

Table 1. Chapter 4 (continuation)

	Month 2 +H2O	+CHO	%	Est.	Dev	X2	P
Formicidae	177.5	174.6	-1.6	-0.02	20.9	0.00	0.947
F-W	159.4	123.6	-22.4	-0.25	21.5	0.63	0.426
Wasmannia	18.1	51.0	181.7	1.04	22.8	1.49	0.222
PREDATOR							
Aranea	10.5	6.2	-40.7	-0.52	18.5	3.09	0.079
Mesostigmatidae	68.2	50.6	-25.7	-0.30	22.4	0.51	0.475
Opiliones	3.7	3.3	-9.9	-0.10	20.9	0.11	0.735
Prostigmatidae	43.4	50.2	15.7	0.15	20.5	0.19	0.662
Pseudoscorpionida	8.4	5.2	-37.8	-0.48	20.6	1.00	0.318
Trombidoidea	3.7	7.1	92.1	0.65	24.9	2.76	0.097
GRAZER							
Collembola	133.7	100.6	-24.7	-0.28	20.5	0.69	0.405
Dipt_Larva	8.9	9.5	7.3	0.07	22.3	0.02	0.890
Hemiptera	11.6	2.8	-75.1	-1.39	18.2	9.08	0.003
Oribatida	581.3	534.7	-8.0	-0.08	20.1	0.09	0.766
Thysanoptera	3.4	5.7	69.9	0.53	20.4	1.23	0.268
SHREDDER							
Diplopoda	20.3	18.8	-6.9	-0.07	21.0	0.03	0.857
Gastropoda	1.4	1.4	3.1	0.03	17.5	0.01	0.935
Isopoda	6.7	5.5	-17.0	-0.19	22.1	0.15	0.697
BIOMASS	Control	+CHO	%			V	P
Litter depth	2.2	2.1	-1.22			25	0.590
Decomp.Filter	70.0	71.6	2.29			22	0.570
Decomp.Popsicle	24.9	30.5	22.49			26	0.720

CHAPTER 5: ASSEMBLY MECHANISMS SHAPING TROPICAL LITTER ANT COMMUNITIES

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Keywords. Brown food webs, ants, ecological traits, phylogeny, competition, scale, ecological filters.

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Abstract

Much of community ecology seeks to unravel the assembly mechanisms allowing species to coexist in space. These mechanisms include those limiting (e.g. ecological filters) and those increasing (e.g. competitive exclusion) the phylogenetic and trait dispersion among species within communities. Here we assessed the relative strength of these mechanisms in tropical litter ant communities by mapping their patterns of phylogenetic and trait (worker and queen size) dispersion. We surveyed ant communities in a spatially nested design that allowed us to 1) explore the spatial scales, from fine (0.25 m^2) to coarse (361 m^2), at which these possible mechanisms act stronger; and 2) assess the contribution of regional species pools, assembled from small (plot) to large (island) pools, in the structure of local communities. Patterns of phylogenetic dispersion in these ant communities suggested that these were composed of more closely related species than expected by a random sampling of the species phylogenetic pool (i.e. clustered). The magnitude of the phylogenetic clustering tended to increase with size of the regional pool but was consistent across spatial scales. Patterns of trait dispersion within communities also showed clustering, and most communities were composed of ant species that were smaller (using both worker and queen size) than expected. Trait clustering decreased at coarser spatial scales, but increased with the size of the regional species pool. Together, these results suggest that ecological filters, not interspecific interactions, are structuring tropical ant communities, favoring clades with small worker and queen sizes. Greater dependency of our results on the size of the regional pools and than in the spatial scale of the observations suggests that environmental heterogeneity is low within our sites but high between

them.

Introduction

Much of community ecology seeks to unravel the assembly mechanisms allowing species to coexist in space (Hutchinson 1959, Diamond 1975, Hubbel 2001, Chase and Leibold 2003). Two sets of assembly mechanisms are typically inferred by the patterns of phylogenetic and trait dispersion present among species within communities (Cavender-Bares et al. 2009, Fukami 2010). One set focuses on niche-based mechanisms (e.g. biotic or abiotic 'habitat filtering') that limit the phylogenetic and trait variability in a community. For example, in North America, the structure of grassland communities is generally shaped by fire frequency (Collins and Glenn 1990). The other set focuses on mechanisms that limit the similarity among coexisting species (e.g. interspecific competition), thus increasing trait and phylogenetic dispersion in communities (Hutchinson 1959; Cavender-Bares et al. 2009). For example, in central Florida, oak communities tend to be composed of species from different clades, and closer species to show less niche overlap (Cavender-Bares et al. 2004). The balance of these processes has been shown to vary among taxocenes and across phylogenetic and spatial scales (Swenson et al. 2006, Cavender-Bares et al. 2009).

Increasing evidence (Kraft et al. 2008, Burns and Strauss 2011) suggests that the composition of local communities depends on the relationship between the assembly mechanisms acting on the community and the degree of phylogenetic signal shown by traits (i.e. the tendency of closes relatives to resemble each other). For example, early observations suggested that limiting similarity mechanisms such as interspecific competition are strongest between closer species due to high niche overlap (Elton 1946,

Hutchinson 1959). But high niche overlap among sister species requires traits to show phylogenetic signal (i.e. phylogenetically conserved, Kraft et al. 2007). Trait and phylogenetic dispersion among communities assembled by competition should thus be highest when traits present significant phylogenetic signal. Instead, when traits present low phylogenetic signal, competition may result in community assemblages that either appear random (i.e. closest competitors are no longer related taxa) or that present a reduced amount of trait and phylogenetic variability (Cavender-Bares et al. 2004). These communities whose species are more closely related than expected are known as 'clustered'. Mechanisms reducing the extent of phylogenetic and/or trait variability, e.g. abiotic or biotic environmental filters, should result in clustered communities when traits important for ecological filtering present significant phylogenetic signal. For example, most cactuses (family Cactaceae), living on deserts, have two important ecological traits: characteristic thorns and photosynthetic stems. Similarly, ants resisting invasion (by other, invasive, ants) are phylogenetically more closely related than expected (Lessard et al. 2010). Alternatively, both field and modeling work suggest that environmental filters may result in communities with even trait dispersion when traits are convergent (Cavender-Bares et al. 2004, Kraft et al. 2007). Assessing the phylogenic signal in functional traits facilitates the identification of assembly mechanisms.

Ecological relationships are usually scale dependent (Wiens 1989). For example, at fine spatial scales (e.g. 10 ha) one bird (Least Flycatcher) reduces the abundance of another one (American Redstart); however, these birds are positively associated at broader scales (Sherry and Holmes 1988). Similarly, different assembly mechanisms

can operate at the same time, but not necessarily at the same spatial scale (Weiher and Keddy 1999). For example, impacts of environmental filters on community composition should appear at spatial scales in concert with the nature of the filter (e.g. soil profiles, physiological demands imposed by the weather, forest management and history). Instead, limiting similarity mechanisms such as competition likely act at smaller scales, where species likely compete more strongly for available resources (Swenson et al 2007, Cavender-Bares et al. 2009). Supporting this framework, Levins and Franks (1982) found that nests of litter ants in a 10 x 10 m plot, in Panama, were evenly dispersed (a pattern consistent with competition). Similarly, both Nipperes and Beattie (2004) and Gotelli and Ellison (2002) reported even dispersion of ant co-occurrences and body size ratios at fine, but not broad, scales.

Few assembly mechanisms are known to shape litter invertebrate communities in brown food webs (BFWs; Swift et al. 1979), and much of the functional diversity presented by these taxa is traditionally assumed redundant (Ayres et al. 2006). However, BFW assemblages are species rich, and perform a diverse set of critical ecological functions (Coleman et al. 2004, Coleman 2008). Exploring the extent of trait variability and the phylogenetic structure among BFW communities can provide insights into evolutionary processes that permit coexistence, allow the myriad of ecological functions in the soil, and sustain the high diversity of most of these webs. For example, ants compete through several trait-based strategies such as chemical and physical weaponry (Andersen et al. 1991), behavioral dominances (Cole 1983, Cremer et al. 2006), worker and colony sizes (Lester et al. 2009), and dominance-discovery trade-offs (Holway 1998), among others (reviewed in Parr and Gibb 2010). However,

with few species-level molecular phylogenies available (but see Moreau 2008), little is know about the phylogenetic signal of functional traits such as body size in ants.

Here we expand this framework for litter ant communities by 1) using two functional traits (e.g. worker and queen size) fundamental to several ecological interactions carried on by ants such as: fight, protection, foraging and diet; 2) using a comprehensive species-level molecular phylogeny to examine the evolutionary history found among these ecological traits; and 3) describing the distribution of functional traits and phylogenetic dispersion present among species in an explicitly spatially-nested design. Sampling ants in a nested design allowed us to explore the effects of increasing habitat heterogeneity with area and the spatial scales at which assembly mechanisms could act more strongly.

Materials and methods

Study location and sampling design

Ant communities were sampled from July to September 2009, on Barro Colorado Island (BCI; 09° 09′ N, 79° 51′ W), a seasonal tropical forest managed by the Smithsonian Tropical Research Institute in Panama. BCI receives ca. 2600 mm of annual rainfall, with nearly 90% of it falling from May to December (Leigh *et al*. 1999). Sampling thus occurred in mid wet season on BCI —a period of high ant activity (Levings 1983, Kaspari 1996b).

We used berlese funnels to extract ants from litter samples harvested across the island in a spatially nested design. This design allowed us to study local ant communities at three spatial scales and simultaneously compare communities at these

scales against increasing regional species pools (Horner-Devine et al. 2004, Wiens 1989). At the broadest spatial scale, we sampled six sites (361 m^2) across the island. We chose the location of these sites to represent most of the variability in soil and forest type encountered within the island (Baillie et al. 2006). Each site was a square area of 19 x 19 m. At intermediate spatial scales, nine plots (9 m^2) were surveyed within each site. These plots were arranged in a 3 x 3 square grid and separated from each other by 5-m. At finer spatial scales, four quadrats (0.25 m^2) were surveyed within each plot. These quadrats were taken from the corners of each plot. All litter in these quadrats was harvested in the field and transferred in plastic bags to the lab to be surveyed manually for colonies and then transferred to berlese funnels for 24 h. We identified all ants to species/morphospecies level using standard regional keys and reference collections in Panama and Oklahoma.

Local communities were built, for each spatial scale, by combining all the species occurrences in nested samples. In total, 216 local assemblages were quantified at the fine (0.25 m^2) scale, 54 assemblages at the median (9 m^2) scale, and 6 assemblages at the large (361 m^2) scale. Each assemblage was characterized by the presence/absence of an ant species (out of 98 species present in our whole survey). Presence/absence is a conservative measure of species composition and assumes that a maximum of one colony per species occur in each 0.25 m^2 quadrat.

Building regional species pools

Our nested design allowed us to compare community composition in our local communities against increasingly large regional species pools. 'Plot' pools consist of all

the species summed across the four quadrats within a plot. We assumed that plot pools represent the arena where most species-level interactions should take place. 'Site' pools consist of all species summed across the nine plots within a site. Site pools are likely responsive to within-island variability in soil profiles and forest history. Finally, the 'island' pool consists of all the species summed across the six sites (i.e. all the species encountered in this study). Because of the nature of a nested design, local communities at each spatial scale were compared with regional species pools above the spatial extent they belong to, such that local communities at finer scales (0.25 m^2) were compared to plot, site and island pools, but local communities at the broader scales (361 m^2) were compared only to the island pool.

Functional traits

We studied two ecological traits (i.e.. worker and queen size) that represent species level characteristics among ant species. Worker size can constrain prey/food particle size, foraging area and defense strategies (Kaspari 1996, Hurlbert et al. 2008). Queen sizes should mirror important colony traits such as starvation resistance and colony growth (Kaspari and Vargo 1995). We used Weber's length to measure queen or worker size. Weber's length is defined here as the distance from the anterior-most part of the ant pronotum, to the posterior most part of the ant metapleuron. We measured between two and five different specimens for a total of 218 worker specimens from 98 species, and 191 queen specimens from 75 species for queen size. All measurements were taken on dry, pinned, specimens using Olympus SZX12 and Olympus SZ51 stereoscopes, with a reticule to the nearest 0.01mm.

Phylogeny construction

We inferred a species-level phylogeny using molecular information. Because a robust species level phylogeny for ants is still not available, we used DNA barcode sequences (COI, cytochrome c oxidase subunit I) and a constraint tree, in an approach similar to that of Kress et al. (2011). This approach allowed us to provide phylogenetic resolution (using DNA barcode) for species within genera, and maintain all the inter-generic relationships in the constraint tree. We chose the phylogeny of Moreau et al. (2005) as a constraint tree because of its ampler coverage of Neotropical taxa and because it includes full DNA barcode sequences. To infer the phylogeny, the DNA barcode dataset included sequences from both the ant species found in our survey of BCI litter and taxa found in Moreau et al. (2005). We estimated a Maximum Likelihood tree (RAxML) using CIPRES and calculated support for the resulting tree using a bootstrap procedure and a GRT+ GAMMA+P-Invar model of substitution. COI barcodes for our ant species were obtained in collaboration with the Biodiversity Institute of Ontario and using sequencing techniques and available analytics tools using tools in the Barcode of Life Database (BOLD, Ratnasingham and Hebert 2007). New sequences for our study were uploaded on the BOLD database (http://www.boldsystems. org/), and are publicly available under the project "DT" named AntsofBCI_1_ProjectCommScal_1.

Phylogenetic signal of ecological traits

We measured phylogenetic signal in worker and queen size using our species-

level phylogenetic tree and the Blomberg's K statistic (Blomberg et al. 2003). Blomberg's K estimates the amount of trait variability within a phylogeny. When K equals 1 the trait distribution on the phylogeny matches a Brownian motion evolution model. This model does not assume that traits are invariable across the phylogeny, rather it assumes that trait variability is proportional to the amount of evolution depicted in the phylogenetic tree. K<1 indicates more trait convergence than expected by the Brownian model (e.g. cases when traits are more malleable than expected). K>1 indicates more trait conservatism than expected by the Brownian model (e.g. cases when traits are less malleable than expected). We assessed the significance of the observed K, by comparing K values to the ones obtained by generating 999 random combinations of traits values in the phylogeny. Using a two-tailed approach, probability values of less than 0.025 indicate significant trait conservatism. The R package 'Picante' (Kembel et al. 2008) was used to perform these calculations.

Phylogeny-based tests of community composition

Phylogenetic analyses of community structure were performed using the species-level phylogenetic tree onto which local communities were mapped. We estimated the level of phylogenetic structure among our communities with two indices: the Net Relatedness Index (NRI) and the Nearest Taxon Index (NTI) (Webb 2000), as implemented in the R package 'Picante'. NRI and NTI allow us to determine if local communities are composed by a random or deterministic (i.e. phylogenetic clustering or even dispersion) subset of the regional pool of species (Cavender-Bares et al. 2009). NRI corresponds to the standardized effect size (multiplied by -1) of the mean

phylogenetic distance (MPD) across all species in the local communities. NRI is more sensitive to deep phylogenetic branching. Instead, NTI corresponds to the standardized effect size (multiplied by -1) of the mean nearest taxon distance (MNTD, i.e. the phylogenetic distance each species in its nearest neighbor in the local community), and it is more sensitive to branching in the tips of the phylogeny. We obtained standardized effect sizes of MPD and MNTD by comparing our observed values to a null distribution generated with 999 null communities, standardized by the standard deviation of the null distribution (Gotelli and Ellison 2002). We considered each local community as significantly clustered or even dispersed if the observed phylogenetic distance was above or below 2.5% of the null distribution of MPD and MNTD, respectively. To construct our null communities we used the null model 'taxa labels'. This null model generates random communities by shuffling the tips in the phylogeny. Null communities were generated from plot, site, and island regional species pools. Two-tailed Wilcoxon tests were used to test whether NRI and NTI values differed from zero.

Trait-based tests of community composition

We inferred assembly mechanisms shaping litter ant communities in BCI by determining the patterns of trait dispersion present among our local communities, using the approach developed by Kraft and Ackerly (2010). First, we calculated two indices sensitive to the breadth in trait dispersion for each local community. These indices, trait 'range' and trait 'variance' of a community, are assumed to decrease in the presence of an environmental filter. Next, we calculated two indices sensitive to the spacing of trait values. One of these indices, the 'kurtosis' of the trait distribution, should decrease with

respect to a normal distribution (i.e. should flatten or grow platykurtic) when traits are evenly spaced. The second index is obtained by dividing the standard deviation of the distance of a given species to its successive neighbor (in trait space) by the observed trait range (hence SDNDr). SDNDr thus measures the evenness of trait distribution among species once you correct for the species present in a given community. If assembly mechanisms such as interspecific competition are acting in a community, the spacing of trait values is assumed to become constant, and both kurtosis and SDNDr are expected to decrease. Moreover, because SDNDr controls for the species present in a community it is adequate to measure the spacing of traits within a background of ecological filtering.

As in our phylogeny-based analyses, we assessed significance by comparing our observed values to a null distribution generated by 999 null communities. Because both assembly mechanisms are expected to reduce the value of our indices, we used one-tailed Wilcoxon tests to test whether the range, variance, kurtosis and SDNDr differed from zero.

Results

Across our 6 sites, we collected 26,234 ant specimens from 98 species in 2,857 events. The most abundant ants where *Solenopsis* morphospecies 'lash4' (n = 4121), *Wasmannia auropunctata* (n = 3647) and *Solenopsis* morphospecies 'JTsp1' (n = 1988). Seventeen uniques and doubletons (between them: *Proceratium micrommatum*, four species of *Gnamptogenys*, and *Acanthognathus ocellatus*) were included in this study.

Pheidole (with 15 species) and *Strumigenys* + *Pyramica* (with 11 species) and *Solenopsis* (with 10 species) were the most species-rich genera.

Phylogenetic signal of ecological traits

Worker size (as measured by Weber's length) varied from 0.28 mm in the species *Carebara panamensis*, to 4.54 mm in the species *Pachycondyla villosa*. Queen size varied from 0.33 mm in the species *Solenopsis terricola* to 3.75 mm in the species *Odontomachus bauri.* Across the litter ants that we found in our survey, worker size was highly correlated with queen size ($R^2 = 0.90$, $p < 0.001$, Figure 1). Ant size (as measured in workers) was weakly but significantly correlated with ant abundance ($R^2 = 0.06$, $p < 0.009$, Figure 1). Both worker and queen Weber's length presented moderate levels of trait conservatism. In particular, worker size ($K = 1.18$, $p=0.001$) was more conserved than predicted by a random Brownian motion; queen size, instead, was slightly more convergent ($K= 0.97$, $p=0.001$; Table 1). Together, our results suggest that worker size is a less malleable trait than queen size.

Trait-based tests of community composition

The median size of workers and queens in an assemblage represented nonrandom subsets of the regional pools. Relative to null communities, local communities tended to be composed by worker and queen ants that were small in size (Figure 3). At fine (0.25 m^2) spatial scales, mean worker size was -0.48±0.94 (results in effect size) when compared to plot pools. Moreover, by increasing the size of the regional pool, these effects were magnified. Mean worker size decreased to -0.75±0.82

when compared to site pools, and it further decreased to -1.14 ±0.72 when compared to island pools. Increasing the scale at which local communities were assembled did not change the results. This is, at median (9 m^2) scales, mean worker size was -0.66±0.89 (results in effect size) when compared to site pools. At this scale, mean worker size further decreased to -1.35 ± 0.68 when compared to island pools. At the largest scale (361 m^2) the pattern was similar; mean worker size was smaller than a random sampling of the regional -island- pool (-1.51±0.66, results in effect size). Results based on queen size generated results that presented similar trends and magnitudes (Figure 3).

Patterns of trait dispersion suggest that sizes of workers and queens were more tightly clumped than predicted from a random sample of the species pool. At fine (0.25 m^2) spatial scales, and when compared to plot pool, worker size, and queen size presented significant levels of clustering (Table 1). The range (worker median = 0.042, $p < 0.001$; queen median = -0.072, $p < 0.001$), and variance (worker median = -0.386, $p < 0.001$; queen median = -0.430, $p < 0.001$), of Weber's length were significantly reduced. Across these communities, no evidence of even dispersion of traits existed, the standard deviation to the nearest distance index (SDNDr) (worker median = 0.115, $p = 1.0$; queen median = 0.043, $p = 1.0$), and kurtosis (worker median = 0.265, $p=1.0$, queen median= 0.070, $p=1.0$) were not significantly reduced. Similar results were present when comparing these communities (from finer scales) to site and island pools (Table 1). The magnitude of trait clustering decreased at medium (9 m^2) spatial scales, neither the range of worker or queen size (worker median = 0.297, $p = 0.981$; queen median = 0.483, $p = 0.989$) nor the variance (worker median = 0.017, $p = 0.428$; queen median = 0.027, $p = 0.378$) were reduced when comparing these communities against site pools

(Table 1). Worker and queen size were clustered when we increased the size of the regional pool and compared these communities with island pools. No evidence was found of even dispersion in communities assembled at this scale. At broader (361 m^2) spatial scales, clustering of worker and queen size traits were weaker, and only worker size presented significantly reduced level of trait variance (median= -0.72, p=0.03) and range (median= -1.18, p=0.05). No evidence was found of even dispersion at this scale, either (Table 1).

Phylogeny-based tests of community composition

Phylogeny-based analysis revealed support for phylogenetic clustering (Figure 2). Species in communities at finer (0.25 m^2) scales were phylogenetically more closely related that expected when comparing them against plot pools (NRI = 0.485, $p<0.001$; NTI = 0.271, $p < 0.001$), site pools (NRI = 0.832, $p<0.001$; NTI = 1.141, $p<0.001$) and island pools (NRI = 1.196, $p<0.001$; NTI = 1.141, $p<0.001$). At this scale the clustering signal increased with increasing size of the regional pool, as represented by increasing median values. At intermediate (9 m^2) spatial scales, species in local communities were phylogenetically more related that expected when comparing against site pools (NRI = 0.624, $p < 0.001$; NTI = 0.833, $p < 0.001$) and island pools (NRI = 1.190, $p < 0.001$; NTI = 1.632, $p < 0.001$). At this scale, the clustering signal also increased with the regional pool. At the largest (361 m^2) spatial scale, when comparing local communities with island pools, they were also phylogenetically clustered, but the trend was not significant (NRI = 1.353, p = 0.094; NTI = 1.459, p = 0.063; Figure 2).

Discussion

In this Neotropical ant community, both phylogenetic- and trait-based analysis revealed non-random, mostly clustered, patterns of community composition. Local communities were composed of a subset of species that were more closely related (in phylogenetic and trait terms) than would be expected by chance. Because we found significant trait conservatism among the two traits studied here, these results suggest that ecological filters are reducing the phylogenetic and trait dispersion at all spatial scales, a pattern that is currently difficult to disentangle with phylogenetic data (Lessard et al. 2010, Machac et al. 2011), trait data (Nipperess and Beattie 2004, King 2007, Sanders et al. 2007, Lester et al. 2009), or species occurrences (Albrecht and Gotelli 2001, Ribas and Schoereder 2002, Sanders et al. 2003) alone.

But why does selection favor smaller ants? Previous research studying global trends in ant sizes suggest that ant colonies in tropical sites rich in NPP (similar to ours) may be small, both in terms of size of workers and total worker number (Kaspari 2005). At least two hypotheses have been proposed to explain why ants in tropical systems are smaller than the temperate counterparts. The first one exploits benefits of small sizes in environments with high metabolic costs, such that smaller ants having shorter developmental times may better compete against large taxa in increased NPP environments (Blackburn and Gaston 1996, Chown and Gaston 1997). The second one posits that small body sizes are a response to predation pressure (Abrams and Rowe 1996), which is known to increase in lower latitudes (Jeanne 1979). Here we showed that ants with small sizes are further selected for within a locality, and that an overrepresentation of small taxa exists at BCI at any given spatial scale. We suggest

that nest limitation produced by the fast decomposing rates of tropical litter environments partially explains these results, such that larger ants may be disproportionally negatively affected in environments in shallow litter or litter with fast turnover rates. Similarly, previous research done in this tropical forest has identified a negative relationship within predator abundance and gradients of litter depth (Donoso et al. *Chapter 2*). Because ants are more predacious in tropical ecosystems than their temperate counterparts (Jeanne 1979), integration of these results should benefit from assessing the relationship between ant size and trophic level, and how these two ecological traits vary across gradients of litter depth.

Our results were affected more by the size of the regional pool than by the spatial scale of our observations. For example, the magnitude of phylogenetic and trait clustering did not increase between scales, but within a given scale it increased with increasing regional pools. The relatively small influence of spatial scale in our analysis was unexpected and suggests that litter heterogeneity, which likely increases in larger areas (e.g. variability of nesting sites, food patches, and diversity of predators, all increase with area), played little role in explaining our results. Alternatively, the strong influence of regional pools on the magnitude of phylogenetic and trait clustering suggest that relevant taxa (e.g. phylogenetically distinct and/or larger taxa) continued adding to the regional pool as this increased from plot of island representation (Swenson et al. 2006, Lessard 2011). Larger taxa are more patchily distributed, a pattern contrary to the one predicted by the grain-size hypothesis (Kaspari and Weiser 1999, 2007). In conclusion, we have demonstrated that litter ant communities at BCI are shaped by deterministic processed limiting and that ecological filters, not interspecific

interactions, are structuring tropical ant communities, favoring clades with small worker and queen sizes.

Figure Legends. Chapter 5

Figure 1. Linear least squares regressions of A) worker size vs. queen size; and B) ant abundance (measured as the number of colonies collected in the present study) against ant size. The coefficient of determination R_2 and the probability p associated to these regressions are given. In B, dotted lines running vertically separate the fourth quartiles of the abundance distribution (Q1 having most of the less abundant –rare– species and Q4 having the few more abundant species). Blue dots represent the average size in the four quartiles.

Figure 2. Phylogenetic relationships of the litter ant species in Barro Colorado Island, Panama. The tree was inferred using the RAxML algorithm, a constraint tree generated from Moreau et al. (2005) and 654 bp of the COI Mitochondrial DNA Barcode. A total of 98 ant taxa and 3 outgroups (in black) are included in this phylogeny. Ant subfamilies are colored (Myrmicinae = pink, Ponerinae = yellow, Ectatomminae = green, Formicinae = blue, Proceratiinae = light blue, Cerapachynae = purple). Final ML Optimization Likelihood: -54901.134757. Proportion of invariables sites was 0.299285. The alpha value for the discrete gamma parameter was 0.468526.

Figure 3. Summary of trait-based analysis of community composition. Boxplots depict distribution of median (effect sizes) values for Worker and Queen Weber's length across all (0.25 m_2, 9 m_2 and 361 m_2) spatial scales and all regional species pools (Pl = Plot, Si = Site, Is = Island, pools). Significant deviation from zero, as summarized by one-tailed Wilcoxon test are colored in blue.

Figure 4. Boxplot of Net Relatedness Index (NRI) and Nearest Taxon Index (NTI) values for all communities. Positive NRI and NTI values means that communities are phylogenetically clustered. Negative NRI and NTI values means that communities are phylogenetically evenly dispersed. Significant deviations from a two-tailed Wilcoxon text are depicted by blue boxes.

Figure 1. Chapter 5

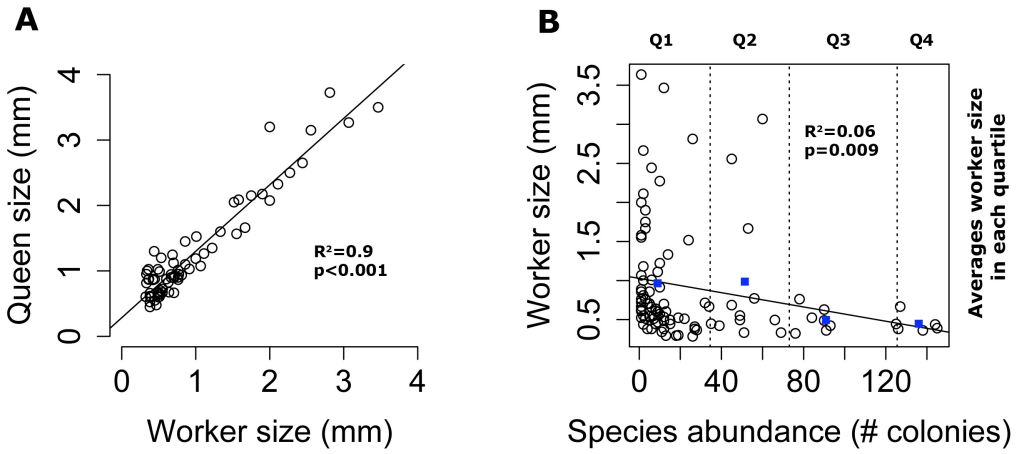


Figure 2. Chapter 5

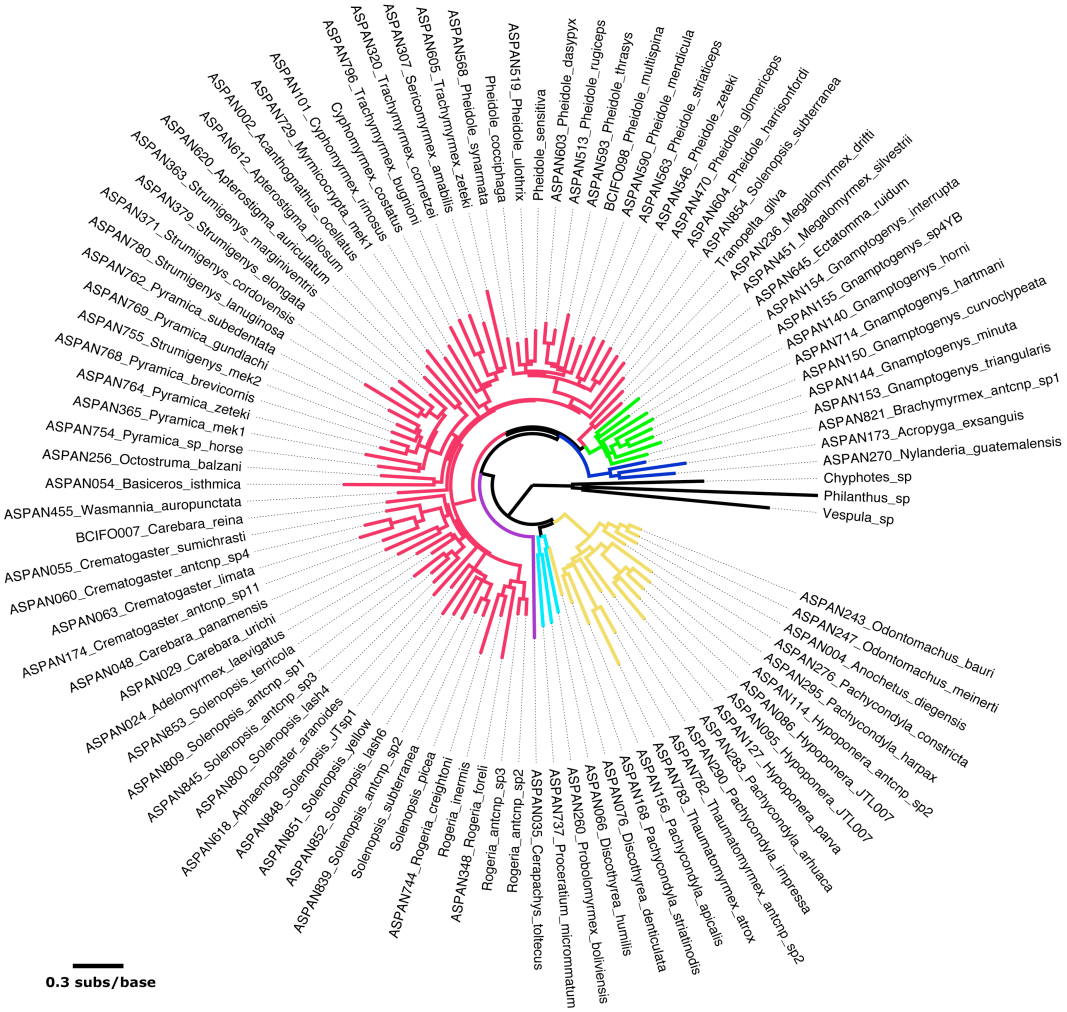


Figure 3. Chapter 5

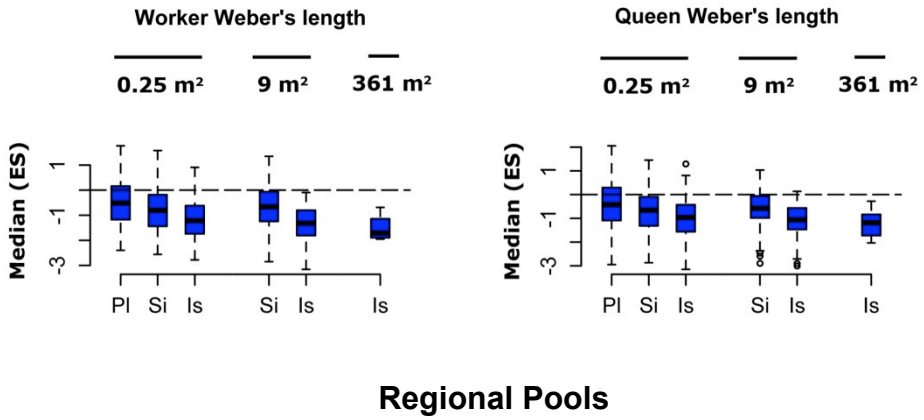
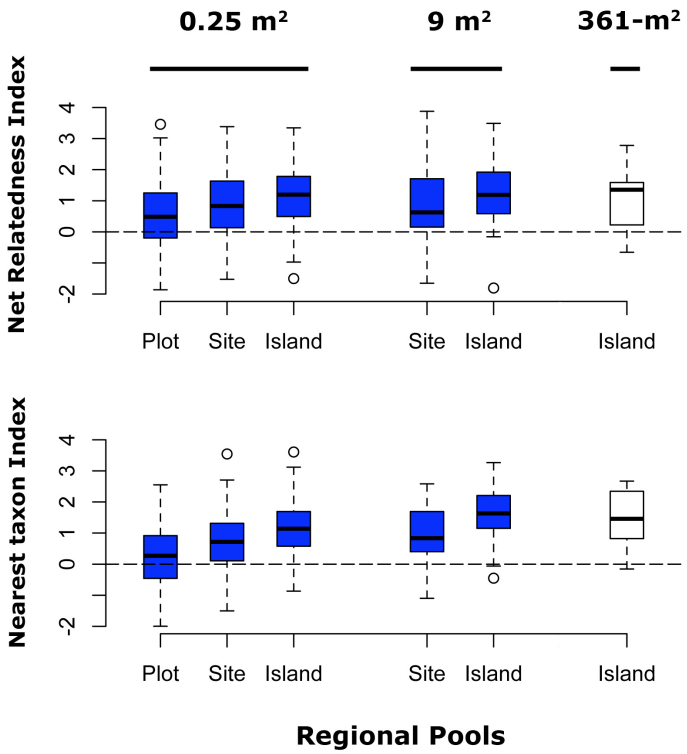


Figure 4. Chapter 5



List of Tables. Chapter 5

Table 1. Results of trait-based analysis. Standard effect sizes and p values for trait range (range), variance (var), the standard deviation of the neighbor distance corrected by the trait range (SDNDr) and kurtosis (kurt). Range and variance are measures sensitive to ecological filtering. Kurtosis is sensitive to interspecific competition. SDNNr is sensitive to interspecific competition within a scenario of environmental filtering.

Table 1. Chapter 5

		Filtering			
0.25 m^2 vs.		**range**	**p**	**var**	**p**
Plot	Worker Size	0.04	**<0.01**	-0.39	**<0.01**
	Queen Size	-0.07	**<0.01**	-0.43	**<0.01**
Site	Worker Size	0.01	**<0.01**	-0.43	**<0.01**
	Queen Size	0.05	**<0.01**	-0.54	**<0.01**
Island	Worker Size	-0.19	**<0.01**	-0.61	**<0.01**
	Queen Size	0.01	**<0.01**	-0.63	**<0.01**
9 m^2 vs.					
Site	Worker Size	0.30	0.98	0.02	0.43
	Queen Size	0.48	0.99	0.03	0.38
Island	Worker Size	-0.10	**<0.01**	-0.42	**<0.01**
	Queen Size	0.05	0.89	-0.19	**<0.01**
361 m^2 vs.					
Island	Worker Size	-1.18	**0.05**	-0.72	**0.03**
	Queen Size	0.61	0.78	-0.83	0.08

Table 1. Chapter 5 (Continuation)

		Even Spacing			
0.25 m^2 vs.		**SDNDr**	**p**	**kurt**	**p**
Plot	Worker Size	0.12	1.00	0.27	1.00
	Queen Size	0.04	1.00	0.07	0.94
Site	Worker Size	0.41	1.00	0.56	1.00
	Queen Size	0.40	1.00	0.30	1.00
Island	Worker Size	0.79	1.00	0.76	1.00
	Queen Size	0.74	1.00	0.62	1.00
9 m^2 vs.					
Site	Worker Size	0.39	1.00	0.28	1.00
	Queen Size	0.52	1.00	0.39	1.00
Island	Worker Size	0.80	1.00	0.82	1.00
	Queen Size	0.97	1.00	1.20	1.00
361 m^2 vs.					
Island	Worker Size	-0.13	0.66	0.60	0.92
	Queen Size	0.13	0.84	1.55	0.98

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