Ants accelerate litter decomposition in a Costa Rican lowland tropical rain forest

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Abstract: The decomposition of leaf litter is governed, in part, by litter invertebrates. In tropical rain forests, ants are dominant predators in the leaf litter and may alter litter decomposition through the action of a top-down control of food web structure. The role of ants in litter decomposition was investigated in a Costa Rican lowland rain forest with two experiments. In a mesocosm experiment, we manipulated ant presence in 50 ambient leaf-litter mesocosms. In a litterbag gradient experiment, *Cecropia obtusifolia* litter was used to measure decomposition rate constants across gradients in nutrients, ant density and richness, with 27 separate litterbag treatments for total arthropod exclusion or partial arthropod exclusion. After 2 mo, mass loss in mesocosms containing ants was 30.9%, significantly greater than the 23.5% mass loss in mesocosms without ants. In the litter bags with all arthropods excluded, decomposition was best accounted by the carbon : phosphorus content of soil ($r^2 = 0.41$). In litter bags permitting smaller arthropods but excluding ants, decomposition was best explained by the local biomass of ants in the vicinity of the litter bags ($r^2 = 0.50$). Once the microarthropod prey of ants are permitted to enter litterbags, the biomass of ants near the litterbags overtakes soil chemistry as the regulator of decomposition. In concert, these results support a working hypothesis that litter-dwelling ants are responsible for accelerating litter decomposition in lowland tropical rain forests.

Key Words: ant, biomass, arthropod, decomposition, detritus, leaf litter, phosphorus, tropical rain forest

INTRODUCTION

In plant-based food webs, energy transfer among trophic levels is regulated top-down by herbivores and their predators, and bottom-up by the resource base (reviewed by Shurin *et al.* 2002). It is unclear how lessons learned from plant-based systems translate to the detrital food web (Moore *et al.* 2004, Srivastava *et al.* 2009). Experimental manipulations of trophic processes in detrital food webs are warranted to resolve this open question.

It is well established that litter decomposition is positively associated with soil and litter nutrient concentrations (Wood *et al.* 2006). Top-down effects are not as well understood. In prior experiments, it has been found that the presence of leaf-litter and soil arthropods speeds up decomposition (reviewed by Bradford *et al.* 2002, Hättenschwiler & Gasser 2005, Moore *et al.* 2004). However, in some cases, litter-dwelling animals have been found to be neutral with

respect to decomposition (González & Seastedt 2001, Heneghan *et al.* 1998), and in other cases may even have inhibitory effects (Hunter *et al.* 2003, Wyman 1998). In tropical environments, fewer studies have been conducted but it appears that arthropods have a stronger positive effect on decomposition (González & Seastedt 2001), perhaps because the arthropods are less subject to abiotic constraints (Heneghan *et al.* 1998).

In tropical forests, both decomposition processes and leaf-litter arthropod communities are remarkably heterogeneous (Kaspari & Yanoviak 2009), reflecting the heterogeneity of the litter itself (Townsend *et al.* 2008). The different functional groups of litter arthropods are expected to have distinctly different effects on the decomposition of litter, and more attention is required to understand the distinct roles of each group (Coq *et al.* 2010, Powers *et al.* 2009), Among the many taxa that inhabit litter, ants are abundant predators (Byrne 1994, Kaspari 1996a, McGlynn 2006, Wilson 2005). Because the functional composition of detritivorous arthropod communities affects decomposition (Hättenschwiler *et al.* 2005), it is expected that ants, depredating consumers,

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may exert a predominant top-down effect. Moreover, there are substantial differences among the diets of litter ants, and the composition of the ant community may result in predation at different trophic levels (Jacquemin *et al.* 2012, Mezger & Pfeiffer 2010, Wilson 2005). Although ants demonstrate high density, biomass and richness in tropical leaf litter (Lach *et al.* 2010), there is scant understanding of how this particular taxon affects decomposition.

Here we report the results of two experiments designed to evaluate the effect of ants on the decomposition of leaf litter in a tropical rain forest. In a mesocosm experiment, we manipulated the presence and mass of ants in 1000-cm^2 leaf-litter mesocosms in situ and measured the fraction of mass loss of ambient litter. In a litterbag deployment, we tested whether ant communities outside the litterbags were associated with decomposition rates constants of a common litter across an ambient gradient of varying ant abundance and nutrient availability. Through the action of a top-down trophic cascade, we expect the introduction of ants into mesocosms to positively influence decomposition, as ants are likely to reduce the density of arthropods that graze on decomposing microbes. In the litterbag gradient experiment, we expect decomposition in a partial arthropod exclusion be positively associated with ant density, biomass and richness. We expect this finding because the locations where ants will have the greatest trophic effect outside the litterbag will result in a decline in overall density of microbivore communities that infiltrate the litterbags, resulting in enhanced decomposition.

METHODS

Work was conducted at La Selva Biological Station, located in north-eastern Costa Rica 10°26′N, 84°00′W. La Selva is located in a lowland tropical wet forest, receiving *c.* 4 m of rain annually (McDade *et al.* 1994). More information about La Selva is available at www.ots.ac.cr.

The mesocosm experiment was conducted at single location in the forest, where previous studies on litter-ant community ecology have been conducted (Kaspari 1996b, McGlynn 2006, 2010; McGlynn & Owen 2002), with respect to the La Selva trail system located *c.* 100 m west of the 750-m mark of the Camino Circular Cercano. Large volumes of standing litter from a 200-m^2 area in the site were collected from the forest floor into several large plastic bags, and were exhaustively searched for individual ants and colonies in an ambient-temperature laboratory. The nests of the colonies contained little to no waste or detritus that may have influenced the decomposition of the litter inside the mesocosms. Ants from all experiments were counted and identified to species or provisional species using taxonomic keys available at www.evergreen.edu/ants. Ant colonies were sorted into three functional categories – generalist foragers (species of *Pheidole, Solenopsis, Wasmannia*), dacetines (mesoarthropod specialists *Acanthognathus, Strumigenys, Pyramica*), and larger-bodied ponerimorphs (*Hypoponera*). Nests were introduced into the mesocosm within a 12-h period.

Mesocosms were composed of 100-μm polyester fabric (Aquatic Eco-Systems, Inc., Apopka, FL, USA) – material fine enough to prevent the entry or egress of ants and other litter mesofauna. The ants in the study have head widths ranging from 0.4 mm to > 1 mm, though the width including legs is notably greater. Mesocosms were sewn with polyester thread into square sacks with sides approximately 32 cm in length, with an area of *c.* 1000 cm^2 per mesocosm. For each mesocosm, standing leaf litter free of termites and coarse woody debris was homogenized by hand in preparation for mesocosms after all ants had been removed by exhaustive hand-searching. Care was taken to maintain the non-ant arthropod fauna of the litter (exclusive of termites) by maintaining ambient temperature and humidity, and to prevent the escape of larger individuals by maintaining samples in a large plastic bag. Ants were introduced into treatment mesocosms, whereas mesocosms with no ants were designated as controls. All mesocosms received supplemental bamboo twigs, which provided nesting space for ant colonies. Ant treatments were separated by functional group and two to four colonies of ants were introduced into treatment mesocosms. The number of colonies of ants varied in a fashion designed to equalize the number of individual ants per mesocosm, as some colonies were larger than others; the exact colony sizes were not known at the outset because the disruption of the twig nests would have adversely affected their survival and performance in the experiment. The mesocosms were completely closed, sealed with monel staples, and returned to the locality from which the litter had been sampled. Twenty mesocosms without ants were created and 30 with ants were created. Ten mesocosms contained dacetines, ten contained generalist foragers, four contained ponerimorphs and six mesocosms contained a combination of three nests, one from each of the three categories. Mesocosms contained moist litter from the field equivalent to 150 g dry mass. Water content was determined using separate subsamples from the source litter, from which litter was extracted and weighed to 1 mg, and then washed and oven-dried at 60°C to constant mass. The subsamples were reweighed and the fraction of per cent moisture lost was used to estimate initial dry mass of the fresh litter, using the mean value for subsample per cent moisture for each cohort of mesocosms created from the same batch of litter.

After 60 d, each mesocosm was collected from the field for the sampling of ants and the estimation of mass loss. After removing all litter from inside the mesocosms, contents were exhaustively searched for ants, which were collected into microcentrifuge tubes, and the additional bamboo nests added to the bag were removed. One of the ant-exclusion mesocosms was excluded because it was ruptured by a branchfall during the experimental period. Some mortality occurred; at the end of the experiment, ants were not found in one dacetine mesocosm, two ponerimorph mesocosms and three of the combination mesocosms. The dry masses of the ants were estimated by counting and drying ants at $60°C$, and the mass of a subsample of a known number was determined ($\pm$ 0.1 μg) to estimate individual mass. For colonies with a small number of individuals that would not allow accurate biomass estimation, we used estimates derived from congeneric ants of equivalent size. The litter from the mesocosms was processed using the method applied to the initial subsamples.

The litterbag gradient experiment was conducted in the CARBONO plot network in old-growth forest at La Selva. The CARBONO plots consist of 18 0.5-ha plots representing known slope and nutrient gradients (Espeleta & Clark 2007). For each plot, soil chemistry was determined for six composite samples of regularly spaced soil cores per 50 × 100-m CARBONO plot. Samples were air-dried and sieved to 2 mm before being analysed at the University of Göttingen, Germany. Total carbon and nitrogen were analysed with a CHN analyser; total phosphorus was found by HNO_3-pressure extraction and ICP-AES (Inductively Coupled Plasma Atomic Emission Spectroscopy). Soil stocks of these nutrients were calculated from mean soil concentrations, adjusted by mean values for bulk density on each soil type, and expressed as molar ratios (e.g. $C:P$, $C:N$). Among these field sites, the concentrations of litter nutrients closely track the concentrations of soil nutrients (Wood *et al.* 2006). The ant community in each plot was characterized using an intensive sampling protocol conducted in May–June 2004 (Bestelmeyer *et al.* 2000); ten 1-m^2 quadrats were sampled at 10-m intervals along a linear transect running the length of each plot, wherein fine leaf litter, reproductive material (flowers, seed pods, etc.) and twigs < 1 cm diameter were collected for the sampling of all ants nesting in leaf litter. For a detailed description of soil and ant sampling, see McGlynn *et al.* (2009a). The dry weight of all ants nesting in the plots was estimated using the same method as in the mesocosm experiment.

Sets of 100-cm^2 mesh litterbags containing common litter were placed in the field to measure site-specific factors, such as soil nutrients or ant communities, that may affect litter decomposition in the CARBONO plots. Each litterbag campaign consisted of three sets of litterbags per plot, placed in evenly spaced points in the plots, each set consisting of five litterbags, each of which contained 10.0 g of freshly fallen, then oven-dried, *Cecropia obtusifolia* litter. This species was selected for the common litter in the litterbag gradient experiment on account of its ability to collect freshly fallen leaves in sufficient quantities, and to minimize the potential influence of secondary compounds on decomposition that may interact with environmental differences along the resource gradient. One bag from each set was arbitrarily selected for destructive sampling along a year-long chronosequence, at intervals of 2, 4, 8, 26 and 52 wk. The contents of the litterbag were processed to measure mass loss using the same methods of the litter inside the mesocosms, and for each plot, the mean mass loss for each time period was used to calculate k, as a negative exponential decay constant in the decay rate expressed as e^{-kt}. One litterbag campaign was conducted in nine plots starting in June 2007, using bags of 2-mm nylon mesh (Aquatic Eco-Systems, Inc., Apopka, FL, USA), hereafter called the partial arthropod-exclusion treatment. Two additional litterbag campaigns, started in June 2006 and June 2007, were conducted with 52-μm nylon mesh (Aquatic Eco-Systems, Inc., Apopka, FL, USA) litterbags, hereafter called the total arthropod-exclusion treatment. The latter campaigns featured the same sites as the prior campaign, plus nine additional plots in the CARBONO network. Values for k generated from the arthropod-exclusion treatment were calculated using the mean of the two litterbag campaigns.

Data analyses were conducted with JMP 8.0.1 (SAS Institute, Cary, NC, USA). In the mesocosm experiment, we conducted a t-test for groups with unequal variances to determine if the proportion of mass loss differed between the bags with ants and the bags without ants. The proportion of mass lost from mesocosms was arcsine-square root transformed, and continuous variables departing from normality were natural logarithm converted. We evaluated whether the abundance of ants – in terms of number of individuals and biomass – was associated with the degree of mass loss using linear regression. Among mesocosms with ants, we conducted an ANCOVA to determine if the relative effect of ant biomass on litter mass loss varied with functional category, using generalist foragers and dacetines which were adequately represented for this analysis.

For the litterbag gradient experiment, we developed a set of competing regression models to evaluate the extent to which nutrients ($C:N$, $C:P$ and $N:P$) and ant communities (individual density, biomass and species richness) accounted for variance in decomposition rate constants. We used AICc and Akaike weights to select the most parsimonious model for the total and partial arthropod-exclusion treatments (Johnson & Omland 2004).

Table 1. Analysis of covariance evaluating the effect of ant mass on decomposition rate in experimental mesocosms, with ant functional category as a cofactor.

| Source	df	F	P
Whole model	3, 17	2.67	0.081
Log-transformed ant mass in mesocosm	1	5.30	0.03
Ant functional category in mesocosm	2	0.11	0.89

RESULTS

In the mesocosm experiment, the mass lost after 8 wk was significantly greater in the treatments with ants than the treatments without ants, as predicted ($t_{40.04} = 2.10$; P = 0.042; $N_{ants\ included} = 29$; $N_{ants\ excluded} = 20$; with ants, 38.9% mass loss $\pm$ 2.0% standard error without ants, 23.6% $\pm$ 2.5%). Among the mesocosms with ants, there was no relationship between the number of ant adults and the mass lost from the mesocosm ($R^2 = 0.01$), though there was an effect of log ant biomass on mass loss ($R^2 = 0.311$; $F_{1,19} = 8.59$; P = 0.009; Figure 1). There was no significant difference in mass lost from mesocosms among ant functional categories, in an ANCOVA model with log ant biomass as a covariate (Table 1).

In the litterbag gradient experiment, the best supported regression model accounting for decomposition rate constants in the total arthropod-exclusion treatment included solely soil C : P (Table 2; Figure 1a). In the partial arthropod-exclusion treatment, the biomass of ants was the sole variable in the most-supported model, accounting for 50% of the variance in decomposition rate constants (Table 2; Figure 1b).

DISCUSSION

In the mesocosm experiment, we found that ants increased the decomposition of ambient leaf litter. In this experiment, the influence of ants was exerted through biomass; there was no effect of the functional role of the ants, based on the coarsely defined groups that we employed. While the role of arthropods in regulating the decomposition of leaf litter has long been established, experiments typically have been limited to exclusion solely through screening or chemical deterrents (Seastedt 1984). By manually subtracting all ants from the experimental mesocosms, we had an ability to gain insight into the functional role of ants in the decomposition process distinct from the rest of the community. The results of prior arthropod-exclusion experiments in tropical forests have yielded a set of mixed results (González & Seastedt 2001); these studies completely or selectively excluded arthropods without respect to taxon or functional role (as in the present litterbag gradient experiment). We suggest that the disparities among
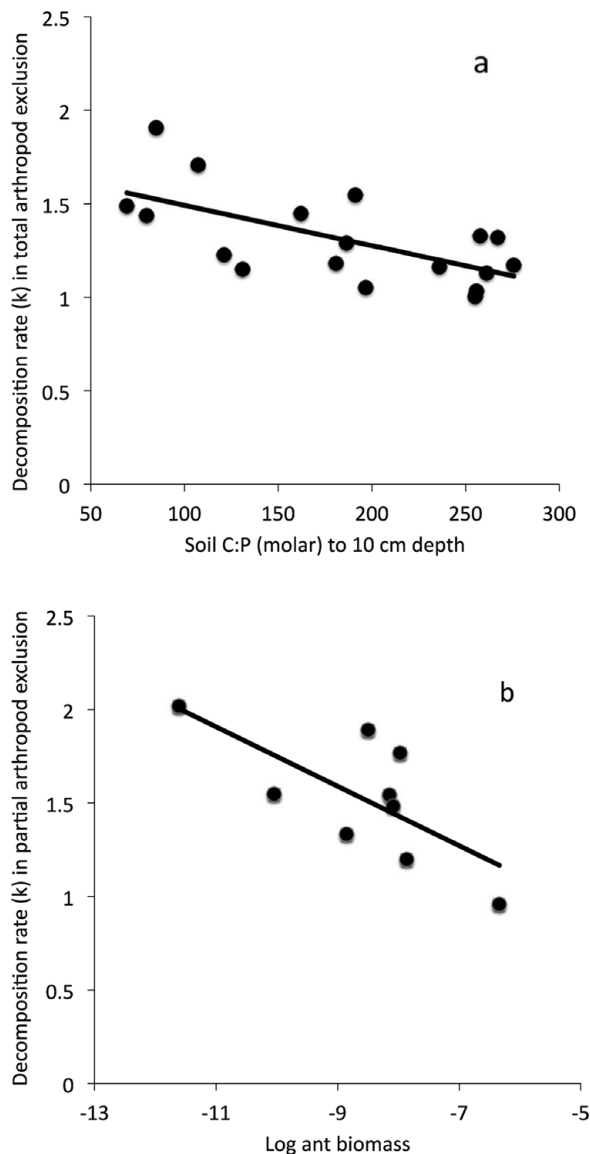
Figure 1. Regression models for decomposition rate constants of leaf litter across a fertility gradient, in litterbags designed for total arthropod exclusion (a) and partial arthropod exclusion (b). Panels indicate the most parsimonious models for decomposition rate constants (Table 2). Regression for total arthropod exclusion: k = 1.71 − 0.002 Soil C : P; for partial arthropod exclusion, k = −0.55 − 0.11 log ant biomass; additional statistics are in Table 2.

prior studies may be explained in part by differences in the relative abundance of ants and other taxa, and the differential effects of the various arthropod-exclusion methods on arthropods with different functional roles in the litter community.

The litterbag gradient experiment results may be consistent with the interpretation of the mesocosm experiment. This experiment was designed so that an increase in the mesh openings would allow some arthropods into the litter, based on body size. No

Table 2. Models for decomposition rates constants of a common litter (freshly fallen *Cecropia obtusifolia*) in litterbags with fine-mesh total arthropod exclusion treatments and litterbags with coarse-mesh partial arthropod exclusion. Environmental parameters for nutrient abundance and ant communities were measured in 18 sites spanning naturally occurring gradients within a tropical rain forest. RSS indicates residual sum of squares; AICc indicates sample-size corrected Akaike Information Criterion.

Variables in model	R^2	RSS	F	P	AICc	Akaike weight	R^2	RSS	F	P	AICc	Akaike weight
			Total arthropod exclusion treatment						Partial arthropod exclusion treatment			
Soil C : N	0.31	0.691	7.21	0.020	−10.9	0.14	0.09	0.394	0.730	0.421	8.19	0.04
Soil C : P	0.41	0.595	10.9	0.004	−14.1	0.68	0.20	0.347	1.77	0.225	7.05	0.06
Soil C : N, soil C : P	0.42	0.583	5.40	0.018	−10.9	0.14	0.21	0.346	0.779	0.500	14.2	< 0.01
Ant density	0.07	0.492	1.21	0.288	−5.99	0.01	0.33	0.290	3.52	0.103	5.42	0.15
log Ant biomass	0.03	0.514	0.453	0.511	−5.19	< 0.01	0.50	0.220	6.88	0.034	2.92	0.51
Ant richness	0.02	0.518	0.341	0.567	−5.07	< 0.01	0.37	0.275	4.09	0.083	4.94	0.19
Ant density, log ant biomass	0.07	0.489	0.614	0.554	−2.74	< 0.01	0.55	0.197	3.62	0.093	9.16	0.02
Ant density, ant richness	0.07	0.929	0.587	0.568	−2.81	< 0.01	0.40	0.262	1.97	0.220	11.7	< 0.01
log Ant biomass, ant richness	0.04	0.507	0.324	0.728	−2.09	< 0.01	0.57	0.186	4.03	0.078	8.62	0.03
Ant density, log ant biomass, ant richness	0.04	0.342	0.075	0.742	1.05	< 0.01	0.58	0.185	2.26	0.199	20.6	< 0.01
All variables	0.46	0.284	2.06	0.141	1.62	< 0.01	0.90	0.039	6.06	0.084	103	< 0.01

arthropods were found in the arthropod-exclusion litterbags. Larger predators were not able to access the contents of the partial arthropod-exclusion litterbags, and no ants were found inside them at the time of collection even though a diverse array of mesoarthropods was inside, including mites and collembolans. In these bags without ants but containing typical ant prey, the most parsimonious explanation of decomposition is, in fact, the biomass of ants in the sites where the litterbags were deployed. This finding indicates that the more ants that are present in a particular locality, the faster decomposition will occur in areas where the ants are excluded. We suggest that the litterbags with partial arthropod exclusion served as enemy-free space for the smaller arthropods, and that in the relative lack of ants and other large predators, the trophic effect of the mesoarthropods was amplified and decomposition was suppressed. The role of mesoarthropods in the litterbag gradient experiment may have been magnified relative to those in the mesocosm experiment, as the common *Cecropia obtusifolia* litter in the litterbags was freshly fallen and subject to more rapid decomposition than the litter in the mesocosms, which was mixed partially decomposed litter derived from mature forest trees. As the addition of ants enhances decomposition in the mesocosm experiment, then in a trophic cascade one would predict that the exclusion of ants would retard decomposition, particularly in sites that have the greatest ambient biomass of ants. As mesocosm experiments featuring predator removal generally have weaker effects than in open-plot experiments (Schmitz *et al.* 2000), we find it reasonable to infer that in the open forest, ants presumably also alter the food web ultimately leading to increased decomposition.

Prior studies have shown that biogeochemistry is a major regulator of litter decomposition in tropical rain forests (Cleveland 2002, Kaspari & Yanoviak 2008,

Kaspari *et al.* 2008). However, biogeochemistry is also a major determinant of the trophic position of ants (McGlynn *et al.* 2009b) as well as ant densities (McGlynn *et al.* 2009a), and even in nutrient-poor areas like our field site, nutrient addition does not necessarily lead to enhanced decomposition (Cleveland *et al.* 2006). In the present study, we found that one biogeochemical parameter which we measured (C : P) was a predictor of decomposition in the absence of arthropods, however the best-supported model featured only ant biomass when consumers were permitted to access litter. It is clear that nutrient availability is important to decomposition processes in tropical rain forests (Cusack *et al.* 2009, Wieder *et al.* 2009), however studies that fail to take into account ant biomass may not recognize the indirect effect of biogeochemistry on the density of top-down control agents such as ants. Because ant densities rapidly respond to changes in their resource base (McGlynn 2006), fertilization experiments are probably inadequate for decoupling the direct effects of nutrients on decomposition and the indirect effect of nutrients via shifts in ant densities.

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