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Bottom-up and top-down regulation of decomposition in a tropical forest

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Abstract The soil nutrients, microbes, and arthropods of tropical forests are patchy at multiple scales. We asked how these three factors interact to generate patterns of decomposition in 450 100 cm^2 litterbags arrayed along a 50 m ridge top in a Panama rainforest. We tested top-down (via grazing by microbivores like collembola and diplopods) and bottom-up (via added N and P) effects on the decomposition of cellulose. By using a 1,000-fold gradient in mesh size we generated a two-fold gradient in arthropod grazing. Microbivore grazing first retarded then ultimately enhanced decomposition rates. Micropulses of N and P (simulating concentrated urine) enhanced neither decomposition rates nor microbivores but increased the abundance of predacious ants. Decomposition rates also varied across the ridge, and were lowest in a plot with the deepest litter and highest soil moisture. These data generate the working hypothesis that N and P cascade upward at grains of 100 cm^2 to enhance a major predator in the litter; predators then absorb any increases in microbivores attracted to the extra fungal growth. These population interactions are in turn embedded in mesoscale variability generated by individual tree canopies that drive changes in litter quality and soil moisture.

Keywords Trophic ecology · Tropics · Fungi · Microbivores · Brown food web

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With few notable exceptions (e.g., Wardle et al. 1995; Scheu and Schaefer 1998; Rosemond et al. 2001), food web ecology has arisen largely from studies of green food webs—plants, their herbivores and predators (Sih et al. 1985; Polis and Hurd 1996). Yet in many terrestrial communities most plant tissue goes uneaten (Coley and Barone 1996). The resulting leaf litter supports the brown (or detritus) food web: a poorly explored biota that includes decomposing microbes (bacteria and fungi) that feed microbivores and, indirectly, their predators (Kaspari 2004). Most aspects of this web, from litter depth (Kaspari 1996b; Vilà et al. 2004) to soil respiration (Kursar 1989) to fungal nutrient concentration (Lodge 1996) to microbivorous invertebrates (Wallwork 1976; Levings and Windsor 1985; Robertson and Freckman 1995; Ettema et al. 1998) and their ant predators (Kaspari 1996a) can vary ten-fold at m^2 grains and 10 m extents. Furthermore, fungi, microbivores and their predators may both respond to and cause changes in rates of decomposition—a key ecosystem process that releases nutrients to the soil and CO_2 to the atmosphere.

An emerging consensus suggests that, at a global scale, decomposition maps onto gradients of climate and nutrient availability (Meetemeyer 1978; Swift et al. 1979; Lavelle et al. 1996; Heneghan 1999; Allen et al. 2005). Less studied is the way that bottom-up and top-down processes create an equally impressive patchiness in local decomposition

rates. Here we explore how nutrient pulses and arthropod access combine to shape decomposition rates of a standardized substrate—cellulose, one of the Earth's most abundant macromolecules—across a ridge top in a Panama rainforest.

Bottom-up effects: nutrient pulses from above

As heterotrophs, litter decomposers are potentially limited by access to N and P (Sterner and Elser 2002). Substrates richer in these elements often decompose faster (Enriquez et al. 1993; Grime et al. 1996) and at the scale of watershed or agricultural field, there is ample evidence that N and P limit decomposition rates (Harmsen and van Schreven 1955; Vitousek 1998; Hobbie and Vitousek 2000; Wardle et al. 2004). Furthermore, these effects can cascade upward, increasing the abundance of microbivores and their predators (Wardle et al. 1995; Scheu and Schaefer 1998; Seagle and Sturtevant 2005; M. Kaspari et al., *Nutrient availability and the regulation of decomposition in a tropical forest*, in review).

A number of processes generate and rearrange the availability of N and P on small scales. First, nutrients constantly rain from the canopy. Fruits (Sevenster and Van Alphen 1993) and leaves (Grime et al. 1996; Cadisch and Giller 1997; Wardle 2002) with their varied nutrient signatures produce a resource mosaic across the forest floor. Urine rich in N and P (Lenter 1981) is regularly deposited by a host of animals, and can cascade up to generate local patchiness in plants and their consumers (Steinauer and Collins 2001). At the same time, in the forest litter such nutrient pulses may be diluted by rainfall, translocated by fungi (Lodge 1996), or otherwise consumed. Their ability to generate patterns of decomposition at 100 cm^2 grains is thus uncertain.

Top-down effects: microbivores and their predators

Unlike the herbivores of the green food web, most litter arthropods do not consume leaf litter directly but instead feed on the decomposer microbes (McFayden 1963), with important implications for decomposition rates (Crossley 1977; Hanlon 1981; Seastedt 1984; Teuben 1991; Wardle and Yeates 1993; Vreeken-Buijs and Brussaard 1996; Scheu and Schaefer 1998; Moore et al. 2003). Such effects on decomposition rates have been posited to be particularly strong in the tropics (Swift et al. 1979).

Two scenarios for arthropod effects been proposed: (1) microbivores act akin to herbivores and eat actively growing fungi, hindering decomposition; and (2) microbivores shred detritus, strip it of senescent mycelia, and/or eat the inhibitory products of cellulose, stimulating decomposition (Hanlon and Anderson 1980; Moore et al. 1988; Teuben 1991). So far it has been difficult to identify which effect predominates, for two reasons. First is the need to reduce arthropod access without simultaneously reducing the microbial turf (Edwards and Heath 1963; Seastedt 1984; Heneghan 1999; Hobbie and Vitousek 2000). Biocides like naphthalene both deter arthropods and decrease fungal biomass (e.g., Williams and Wiegert 1971; Seastedt and Crossley 1983; Blair et al. 1989; Beare et al. 1990; Heneghan 1999). Litterbags made from increasingly fine mesh can deter arthropods but may also hinder microbial colonization or make litterbags increasingly "leak-proof" (Harmon et al. 1999). In this way, standard litterbags and biocides can bias decomposition results toward the second scenario—that of facilitating decomposition.

A second complication is that microbivore effects may also be context-specific, depending on the balance of grazing intensity to microbial activity (Hanlon and Anderson 1980; Moore et al. 1988; Teuben 1991). For example, if the microbial turf is thin and patchy, microbivore grazing rates may exceed microbial growth rates and thus slow decomposition (Dowding 1976; Georgieva et al. 2005). As the balance swings toward faster microbial growth, then decomposition may be enhanced by the cropping of senescent fungal tissue (Hammel 1997). In the wet season of a tropical rainforest, high levels of moisture and warm temperatures (Meetemeyer 1978) favor the latter scenario; that is, fungal regrowth exceeds consumption rates.

Less explored (and in contrast with studies of green food webs, Schmitz et al. 2000) is the role that predators of microbivores play in decomposition. Long-term studies of decomposing sawdust have implicated predacious nematodes in generating food web patchiness (Wardle and Yeates 1993). Predators recruit to nutrient patches (or, more specifically, to the microbivores that gather to eat the sedentary microbes growing at these patches, Chen and Wise 1999). In doing so, they may hinder the accumulation or even lower the number of microbivores on nutrient-enriched patches, effectively removing the nutrient's signal from the intermediate trophic level (Oksanen et al. 1981; Moen and Oksanen 1991; Power 1992).

Here we report the results of a field experiment in a Panama rainforest in which micropulses of nutrients and arthropod abundance are simultaneously manipulated. We used a standard common substrate, cellulose from filter paper. Our goal was to minimize the confounding effects of litterbags while simultaneously evaluating top-down (predators on microbivores and microbivores on microbes) and bottom-up (nutrient availability) factors that can shape local decomposition rates. Specifically, we tested the following predictions: (1) that a single localized pulse of inorganic N or P enhances local decomposition and cascades up

the food web; and (2) that increasing access to substrate by microbivores facilitates rates of decomposition. We further tested for two potential biases of the litterbag method: that finer mesh (1) enhances moisture retention and (2) inhibits colonization by fungi and thus hinders decomposition.

Methods

Three study plots followed a ridge top through closed canopy, old second growth forest on Barro Colorado Island (BCI) in the Republic of Panama (9°9′N, 80°9′W). BCI, a moist tropical forest, receives ca. 2,700 mm of rain annually, and received a monthly average of 334 mm/month (Leigh et al. 1996; Paton 2004) over the eight weeks of this study beginning in June of 2004.

We measured decomposition as mass loss from 2.2 g (five sheets) of coarse filter paper (100% cellulose, Fisher 09-795C) stuffed in 10 × 10 cm litterbags. Cellulose is the main structural component of plant tissue and is attacked by wide variety of fungi (Dix and Webster 1995) and bacteria (Sylvia et al. 1999). All litterbags had polyester, 100-micron pore polyester bottoms. We systematically varied two factors posited to limit decomposition: nutrients (via fertilization) and microbivore access (via different sizes of mesh). In an ancillary treatment, we examined how fine mesh bags may hinder microbial colonization of the substrate.

Microbivore access

We sewed one of four polyester or nylon fabric tops—mesh sizes: 100 microns, 0.25 mm, 1.5 mm, and 12 mm—to the 100-micron bottoms using black polyester thread. This varied access through the top of the bag to arthropods varying 1000-fold in cross-section but maintained the same operational definition of decomposition (loss of cellulose through respiration, translocation, or percolation through the 100-micron bottoms, Harmon et al. 1999). Litterbags were loaded with filter paper in the lab. In the field they were inoculated with 0.2 g of soil and secured to the ground with a PVC flag (litterbags of 100 micron and 0.25 mm mesh were left open on one side to facilitate inoculation, then folded over and stapled shut with five stainless steel staples).

An extra 100-micron litterbag treatment was left uninoculated to test the hypothesis that mesh hinders microbial colonization, resulting in lower decomposition rates in the uninoculated bag.

Nutrient micropulse

Nitrogen and phosphorus, two key macronutrients in ecology (Sterner and Elser 2002), were used as the basis of two nutrient micropulses. Dosages were scaled down to 10 cm^2 versions of those applied to study nutrient limitation in forest ecosystems (Binkley 1986; Tanner et al. 1992; Vitousek et al. 1995). A litterbag thus received one of three nutrient treatments: (1) 5 ml of N solution (0.29 g NH_3NO_2 in 5 ml distilled H_2O); (2) 5 ml of P solution (0.52 g $Ca(H_2PO_4)_2$ dissolved in 5 ml distilled H_2O); or (3) 5 ml of distilled water. The N pulse is about three times the concentration of human urine (7–9 g l^{-1}, Lenter 1981; Kirchmann and Pettersson 1994); the P pulse is considerably stronger, about 300× that of human urine (ca. 0.2 g l^{-1}, Lenter 1981; Kirchmann and Pettersson 1994). However, the quantity of urine deposited from the canopy in one event by a large monkey on BCI is considerably more than 5 ml (Kaspari, personal observation), and thus likely delivers more N and P per event than would be delivered by 5 ml of human urine. The nature of this urine rain remains elusive and understudied.

Nutrient treatments were administered by emptying a syringe directly onto the top of sealed bags. All bags were then covered with a layer of leaf litter.

Experimental layout, monitoring and harvesting

One replicate ([four mesh sizes + one uninoculated bag] × three nutrient treatments) yielded 15 litterbags, which were placed 0.5 m apart in a row. Rows, in turn, were 1 m apart. Within the row, treatment sequence was randomized. Each of the three 10 × 10 m sites, 10 m apart, received ten replicates (150 litterbags). We harvested ten of the 30 rows (= ten replicates) in a stratified fashion after one, four, and eight weeks.

One problem with litterbags is that they can alter the microenvironment, which in turn can shape decomposition rates (Witkamp and Olson 1963). We monitored microclimate using four litterbags of each mesh size loaded with filter paper and placed in each corner of the three sites. Twice a week, at sunrise and midday, the bags were swapped out. The temperature inside the bag was measured immediately with a soil probe thermometer; litterbags were then placed in a drying oven for two days. Moisture was measured as (filter paper dry weight at 60 °C)/(wet weight).

Bags were harvested on weeks one, four, and eight. Litterbags were cleaned of debris and placed in separate plastic bags. Bags were split with scissors and placed in a Berlese funnel to extract arthropods in weeks one and four. After extraction, filter paper was dried at 60 °C for 48 h, and then weighed.

To follow up on site differences, in June 2006 we measured four variables linked to abiotic factors limiting decomposition (Swift et al. 1979)—insolation, soil moisture and pH, and litter depth—at each site. Two parallel transects, equidistant from two corners, crossed each

10 × 10 m site. Five sample points were flagged on each transect every 2 m. At each sample point, we measured %-open canopy using a spherical densiometer. Litter depth was measured by inserting a calibrated stiff wire through the litter until it reached mineral soil. A 10-cm soil core was excavated at each sample point, a subsample was measured for soil pH, and the rest dried to stable weight at 60 °C to measure soil moisture.

Data analysis

Arthropod abundance was recorded from week 1 samples when the cellulose substrate was still abundant and relatively uniform across treatments. We focus here on common taxa grouped by feeding behavior (Swift et al. 1979; Seastedt 1984): collembola, oribatid mites and diplopods (microbivores), and gamasid mites and ants (predators). These groups represented 80% of the total arthropod catch and their abundance was $\log_{10}$-transformed. Inoculation affected only collembola abundance (6.1 vs. 4.2 collembola/bag, Kruskal Wallis $P = 0.025$), so we chose to maximize statistical power by analyzing the effect of $\log_{10}$ mesh size and nutrient treatment (and their interaction) only with site as a blocking variable using a general linear model (SAS 1995). We treated each as a categorical variable, and used orthogonal contrasts to evaluate the shape of the curve relating mesh size to arthropod abundance.

Decomposition for each litterbag was measured as the proportion of remaining dry mass. These values were arcsine-square-root-transformed to improve normality and compared in a general linear model for effects of nutrient (N, P vs. control), and inoculation (presence or absence in the 100 micron mesh bags only); $\log_{10}$ mesh size was used as a covariate. We blocked on site (1, 2, or 3). We performed this analysis separately for each week.

Site abiotic characteristics were compared with analysis of variance and Tukey a posteriori means comparisons.

Results

As assumed, the mesh treatment regulated arthropod access to the substrate (Fig. 1): total arthropod abundance doubled from a mean of 15.8 in the 100-micron mesh to 37.2 arthropods in the 12-mm mesh. This increase was statistically uniform across the three microbivores and two predators (Table 1, mesh effect $P < 0.02$, linear contrast $P < 0.002$), although oribatid mites, gamasid mites, and diplopods approximated a sigmoidal increase (cubic contrasts $0.05 < P < 0.10$). Collembola, the most common microbivore, nearly tripled in number (from 5 to 14 collembola/litterbag) over the 1000-fold increase in mesh size. These increases in arthropod abundance were not confounded by change in temperature or humidity. Litterbag temperature varied from 24.3 to 26.3 °C in the early morning and from 25.6 to 26.9 °C in the afternoon, but failed to vary with mesh size (ANOVA: AM: $F_{(3,20)} = 0.0005$, $P = 0.999$; PM: $F_{(3,20)} = 0.015$, $P = 0.997$). Likewise, water content of the substrate varied from 71.3 to 74.9% in the morning and from 72.2 to 74.6% in the afternoon, but did not vary with mesh size (AM: $F_{(3,20)} = 0.033$, $P = 0.992$; PM: $F_{(3,20)} = 0.103$, $P = 0.958$).

Decomposition varied considerably across the 150 bags sampled in a given time block (0–18% mass loss in week 1, week 4: 0–95%, week 8: 13–100%, Fig. 2). Upon collection, litterbags were frequently fixed to the surrounding leaves and soil by strands of fungal mycelia. The filter

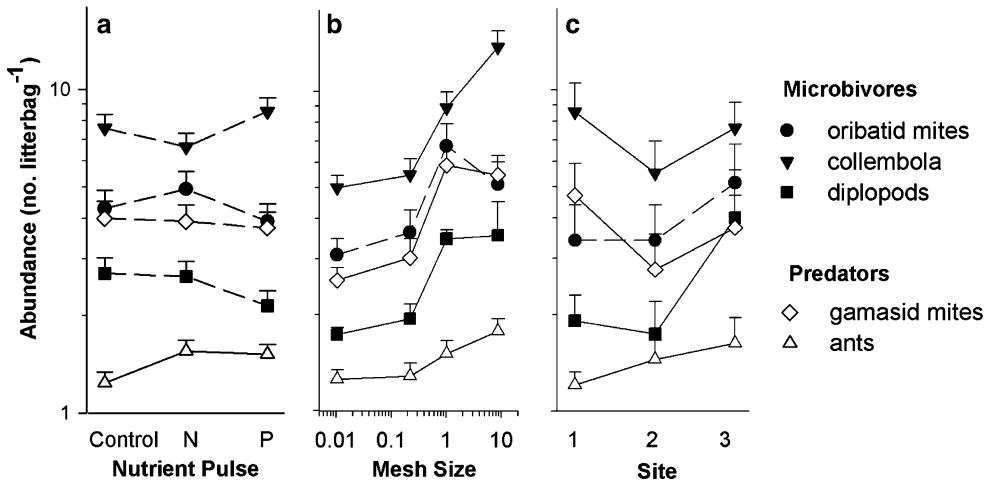

Fig. 1a–c Abundance (means ± SE) of common microbivore (*solid symbols*) and predator (*open symbols*) taxa extracted from litterbags with **a** nutrient pulse (control, N, P), **b** mesh size ranging from 0.01 to 12 mm, at **c** three sites in a Panamanian rainforest in 2004. Significant effects (at $P < 0.05$) are indicated by *solid lines*

Table 1 A general linear model analysis of site (plot 1, 2, or 3), nutrient pulse (N, P or control with distilled H_20), and mesh size (100-micron, 0.25-mm, 1.5-mm, 12-mm), on the abundance of five common arthropods, grouped as microbivores or predators. Orthogonal contrasts measure the shape of the mesh size response. Total $N = 150$

Effect											
Arthropods	Site		Nutrient pulse		P × M		Mesh size		Contrasts		
	F	*P*	*F*	*P*	*F*	*P*	*F*	*P*	1°	2°	3°
Microbivores											
Collembola	5.8	**0.004**	1.9	0.15	0.7	0.67	18.0	**0.000**	**0.000**	0.115	0.451
Oribatids	2.4	0.092	0.9	0.41	0.2	0.99	6.7	**0.000**	**0.001**	0.14	0.052
Diplopods	18.2	**0.000**	1.2	0.32	0.4	0.88	10.0	**0.000**	**0.000**	0.76	0.09
Predators											
Gamasids	4.9	**0.009**	0.1	0.94	0.9	0.50	10.9	**0.000**	**0.000**	0.41	0.057
Ants	4.7	**0.011**	2.5	**0.043**	1.2	0.32	3.6	**0.016**	**0.001**	0.447	0.76

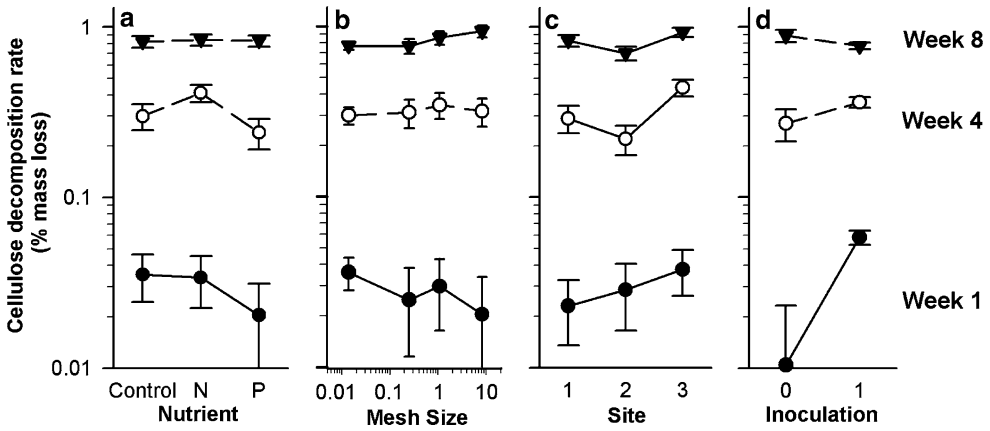

Fig. 2a–d Decomposition rate of cellulose (measured as mass loss, LS means ± SE) in litterbags after one, four, and eight weeks with **a** nutrient pulse (control, N, P), **b** mesh size (ranging from 0.01 to 12 mm), **c** at three sites along a ridge in old second growth forest, and **d** without and with inoculation of 0.2 g of soil at the outset of the experiment. Significant effects (at $P < 0.05$) are indicated by *solid lines*. Note logarithmic scales on mass loss and mesh size

paper was rarely chewed on the edges suggesting the action of large shredders. In most cases of late stage decomposition, a residual film of cellulose lined the 100-micron bottoms, suggesting that the cellulose slipped through the micromesh and was consumed and respired by microbes.

Bottom-up effects

After one week, control and N treatments had equivalent cellulose loss (3.5 and 3.4%, respectively, Table 2). P additions decomposed less (2%, overall nutrient effect $P = 0.022$, Fig. 2) in week 1, but this effect disappeared thereafter.

The abundances of three key microbivores in this system—diplopods, oribatid mites and collembola—did not increase with N and P pulses ($P > 0.15$, Table 1, Fig. 1). The abundance of tiny predacious gamasid mites (which consume other small arthropods) was also invariant across N and P pulses. In contrast, the ants, a larger ubiquitous predator of the litter, increased by ca. 25% with both N and P. Over 50% of these ants were small species of the genus *Pheidole* (e.g., *ruida*, *multispina*, *rugiceps*) that specialize on oribatids and collembola, but do not consume large diplopods (Byrne and Levey 1993; Wilson 2005; Kaspari and Dowling, unpublished data).

Table 2 A general linear model analysis of nutrient pulse (N, P or control by distilled H_20), inoculation (0.2 g soil added or not added to 100-micron bags), mesh size (100-micron, 0.25-mm, 1.5-mm, 12-mm, treated as covariate), and site effects (plot 1, 2, or 3) on decomposition rate over one, four and eight weeks. $N = 150$ for every week sampled. Effects varied over the course of the experiment

Effect	df	Week 1		Week 4		Week 8	
		F	*P*	*F*	*P*	*F*	*P*
Nutrient	2	3.95	**0.022**	1.51	0.224	0.05	0.953
Inoculation	1	81.62	**<0.0001**	1.98	0.162	3.02	0.085
Mesh Size	1	6.9	**0.010**	0.2	0.657	7.42	**0.007**
N × I	2	6.02	**0.003**	0.34	0.711	1.07	0.347
M × N	2	0.43	0.651	0.09	0.918	0.05	0.955
Site	2	3.89	**0.023**	8.09	**0.001**	13.06	**<0.0001**

Top-down effects

The doubling of arthropod abundance with mesh size was associated first with lower then higher rates of decomposition (Fig. 2, Table 2). At week 1, decomposition rate dropped 55% from 3.6% in 100-micron mesh to 2% in 12-mm mesh ($P = 0.010$). Filter paper at this point still had it original rough texture, and the five sheets could be easily peeled apart. By week 4, mesh size effects had vanished ($P = 0.657$). By week 8, decomposition rate was highest in the largest mesh size ($P = 0.007$, Fig. 2), increasing from 77% in the two smallest mesh bags to 94% percent in the 12-mm mesh. This remaining filter paper was usually partially liquefied and showed conspicuous strands of melanized hyphae.

Site effects and dispersal limitation

The location of the litterbag along a 50 m stretch of ridge top proved surprisingly relevant to decomposition rate (Fig. 2, Table 1). In each week, site 3 showed the highest amount of mass loss, from week 1 (almost 60% higher than site 1, $P = 0.023$) to week 4 (twice as high as site 2, $P = 0.001$) to week 8 (30% higher than site 2 ($P < 0.0001$). Summing across all arthropods, abundances were lowest in site 2 and highest, by about 50%, in site 3 (means of 16.6 vs. 27.6/litterbag, respectively).

A subsequent study of the three sites (Table 3, see electronic supplementary material) showed significant heterogeneity in litter depth, soil moisture (but not pH) and canopy openness. Site 3 was intermediate in all three values, and had a thicker understory (Kaspari 2006). Site 2, with the lowest arthropod abundance and decomposition rate, was under the canopy of two 40-cm Diameter at Breast Height *Astrocaryum* palms, whose large fronds (>20 kg) were strewn about the area. Site 3 was under the canopy of a 2 m DBH *Ceiba*, Site 1 was under a series of lianas held up by a variety of 20-cm DBH treelets. Leaves at these sites were considerably smaller and in a more advanced state of decay.

Table 3 Comparison of litter depth, soil moisture, soil pH, and insolation across three sites, 10 m apart, used in this study. Post-hoc Tukey comparisons used to compare means; values sharing a letter are not different at $P < 0.05$

Site	Litter depth (cm)		Soil moisture (% H20)			Soil pH		Insolation (% open canopy)		
1	1.1	a	34	a	b	6.5	a	3.8		b
2	3	b	34.8	a		6.5	a	6.2	a	
3	1.6	a	31.9		b	6.6	a	4.6	a	b
$F_{3,27}$	12.7		7.9			0.5		3.9		
P	0.0001		0.0022			0.6235		0.0327		

The 100-micron mesh fabric could by itself prove a barrier to colonization by fungi (and the collembola that feed on them). Decomposition rate was initially five times lower in these fine mesh bags when the 0.2 g of soil inoculation was omitted: filter paper without this inoculation averaged 1% mass loss (Fig. 2). The trend toward higher decomposition with inoculation was insignificant after four weeks, with some indication of a reversal (i.e., lower decomposition with inoculation, $P = 0.085$) by week 8.

Discussion

Nearly every part and process of the brown food web varies ten-fold or more at grains from 1 m^2 to hectares. At the global scale, abundance and decomposition are more and more linked to climate-induced patterns of productivity and respiration (Meetemeyer 1978; Aerts 1997; Gholz et al. 2000; Kaspari et al. 2000; Kurka et al. 2000; Cebrian and Lartigue 2004; Allen et al. 2005; Seagle and Sturtevant 2005). However, the microbes and invertebrates that do the decomposing interact at much smaller grains (Swift 1987). Along 50 m of a Panama ridge top an array of 450 litterbags reveal that these interactions may shape decomposition at grains of square centimeters. Microbivores facilitated ca. 20% of the decomposition in 100 cm^2 litterbags, while pulses of N and P simulating concentrated urine did nothing to facilitate decomposition but did attract a dominant predator of microbivores. These population interactions, in turn, were embedded in forest structure at the 10 × 10 m scale, which generated patchiness in soil moisture and arthropod abundance.

Bottom-up and top-down interactions at grains of 100 cm^2

The first process generating patchiness in falling leaves may be exposure to the spores and hyphae. Early in the colonization process, access to soil inocula limited decomposition five-fold (Fig. 2)—leaves contacting bare soil may thus get a head-start via contact with a large, active microbial community. During this colonization phase, microbivores appear to keep decomposition in check by recruiting faster than the fungi and bacteria can colonize and grow (Dowding 1976; Georgieva et al. 2005). It is also possible that early colonizing fungi and bacteria, like their plant counterparts (Coley and Barone 1996), may be less defended and more prone to microbivory (Dix and Webster 1995). This inhibition phase appears to be short-lived, however, as are inoculation effects.

The proliferation of mycelia that release decomposing enzymes must ultimately be self-inhibiting, because cellulolytic enzymes slow as the breakdown product glucose accumulates (Hammel 1997) and because senescent hyphae

tend to accumulate, crowding out actively growing hyphae (Dix and Webster 1995). Microbivores, in turn, can slow this effect by harvesting both glucose and senescent hyphae (Hanlon and Anderson 1980; Moore et al. 1988; Teuben 1991). On this Panama ridge top, we see the switch from microbivore inhibition to facilitation beginning at week 4. This facilitation is comparable (but much faster) than leaf litter decomposition from a series of temperate zone studies (Seastedt 1984) and at least one pair of tropical forests (Heneghan 1999). To our knowledge, this is the first study aimed at detecting facilitation in litterbags whose design does not confound access with "leakiness" (Harmon et al. 1999), that quantifies the assumption that increasing mesh size leads to greater arthropod access, and that rules out microclimate effects across mesh size. Moreover, the switch from inhibition to facilitation midway through decomposition may explain, to some degree, the variety of microbivore–decomposition effects reported in the literature (Gessner and Chauvet 1994).

A host of arthropod taxa inhabit the litter (Levings and Windsor 1985), and the isolation of taxon-specific effects on decomposition is beyond the scope of this study. Litterbags in a nearby forest showed a correlation ($r = 0.48$) between arthropod number and mass loss from leaves (Sayer et al. 2006). In this study, increases in collembola (and to a lesser extent, diplopods, Fig. 1) with mesh size best mirror increases in end-stage decomposition (Fig. 2); site 3, the plot with the highest decomposition rates, also had three times as many diplopods. Given the access of litterbags to all common taxa, microcosm studies (e.g., Wiser 1966; Hanlon and Anderson 1980; Teuben 1991) will likely be needed to tease apart their contributions to decomposition.

Large-grain N and P additions (e.g., through oceanic aerosols, rock weathering, or human causes, Stallard 1995) may indirectly shape decomposition via changes in leaf litter quality (Hobbie and Vitousek 2000). Here we focused on nutrient pulses closer to the scale of the urine that regularly rains to the forest floor, targeting fungal populations with N, P and a variety of micronutrients. The bottom-up effects of N and P on decomposition have never to our knowledge been explored at 100 cm^2 grains (but see Scheu and Schaefer 1998 for N-enhancement of litter microbes at the 1 m^2 grain). Contrary to studies at larger grains (Seastedt 1984; Scheu and Schaefer 1998; Hobbie and Vitousek 2000; Franklin et al. 2003), we found no increase in cellulose decomposition with N or P, only a short-lived inhibition of decomposition by P (Fig. 2, $P = 0.02$). This could reflect an allocation by fungi of P into defenses, antibiotics, or fruiting bodies (Stahla and Christensen 1992; Dix and Webster 1995), or more simply, the toxicity of the P fertilizer before rainwater dilutes it.

The lack of an N and P effect in weeks four and eight ($P > 0.22$) would seem to arise from a similar mechanism: nutrients added at this scale are quickly diluted or translocated by extant mycelial networks (Kirk and Farrell 1987; Lodge 1996). However, this would fail to account for the significant increase in predacious ants in N and P litterbags. Litter ants can reduce the densities of collembola, mites, and spiders in this system (Lawrence and Wise 2000; M. Kaspari et al., *Nutrient availability and the regulation of decomposition in a tropical forest*, in review), suggesting a second scenario: N and P enhanced the growth of microbes on cellulose, which in turn attracted microbivores, which in turn attracted a common predator in the litter, the ants. Nutrient pulses can skip trophic levels when predators absorb increases in their prey (Hairston et al. 1960; Oksanen et al. 1981; Power 1992; Kaufman et al. 2002). If this is the case, we observed the microbivores transferring nutrients and biomass between the fungi and the ants via ant predation. Nutrient pulses protected from predators, in contrast, would be predicted to enhance microbivores and decomposition.

The spatial scale of nutrient additions may be key to the subsequent trophic dynamics. While this study suggests that small nutrient patches allow large mobile predators to track and harvest recruiting microbivores, P additions along 40 m stream reaches in Costa Rica (Rosemond et al. 2001) and 40 × 40 m plots in Panama (M. Kaspari et al., *Nutrient availability and the regulation of decomposition in a tropical forest*, in review) enhance microbivore abundance. An array of urine patches may thus be cafeterias that are regularly monitored and cropped by colonies of ants. Larger and more continuous additions of N and P, on the other hand (for example seasonal litterfall or aerosol deposition), would swamp the ability of predators to absorb the resulting increases in their microbivore prey (Power 1992).

Variation at grains of 100 m^2

Three plots, 100 m^2 each, straddled 50 m of ridge top and accounted for 50% of the variation among litterbags aggregated at this grain. Two of the three microbivores tended to lower densities on site 2, which also had the lowest decomposition rates. When studied two years later, site 2 had the deepest litter, highest soil moisture, most open canopy and clearest understory. This appeared to result from two large (>40 cm DBH) *Astrocaryum* palms, whose large fronds knock down other understory plants when they fall and accumulate on the forest floor (Farris-Lopez et al. 2004). Such litter can also immobilize nutrients as basidiomycete fungi translocate soil nutrients to these large carbon sources (Lodge 1996), effectively slowing decomposition elsewhere (Zimmerman et al. 1995). In contrast, site 3, with the highest decomposition rates, had the lowest soil moisture, intermediate depth litter and a thick understory, as well as almost threefold more diplopods. Thus variation at 100 m^2

grains may be driven by the sources of litter themselves—tropical tree canopies—whose footprints for a 40-cm DBH tree can range from 29 to 300 m^2 (Bohlman and O'Brien 2006).

Patchiness in nature is hierarchical, often with bioclimatic processes that drive regional patterns that are further modified by population interactions at finer grains (MacArthur 1972; Pickett and White 1985; Levin 1992). Decomposition seems no exception. Other factors, like the subtle changes in moisture availability that track microtopography, fluxes in abundance of the major players with degradative succession (Swift 1987; Wardle et al. 1995), and the natural churning of population interactions in space (Levin 1992; Keeling et al. 2000), make the brown food web a complex but tractable system for studying patchiness (Moore et al. 1988; Wardle 2002; Kaspari 2004). In this patch of tropical rainforest, the fluid nature of decomposition across the forest floor likely drives and reflects the patchiness of many populations of the brown food web.

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