Arthropod Abundance and Diversity in a Lowland Tropical Forest Floor in Panama: The Role of Habitat Space vs. Nutrient Concentrations

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ABSTRACT

Tropical forest floor characteristics such as depth and nutrient concentrations are highly heterogeneous even over small spatial scales and it is unclear how these differences contribute to patchiness in forest floor arthropod abundance and diversity. In a lowland tropical forest in Panama we experimentally increased litter standing crop by removing litter from five plots (L −) and adding it to five other plots (L+); we had five control plots. After 32 mo of treatments we investigated how arthropod abundance and diversity were related to differences in forest floor physical (mass, depth, water content) and chemical properties (pH, nutrient concentrations). Forest floor mass and total arthropod abundance were greater in L+ plots compared with controls. There were no treatment differences in nutrient concentrations, pH or water content of the organic horizons. Over all plots, the mass of the fermentation horizon (Oe) was greater than the litter horizon (Oi); arthropod diversity and biomass were also greater in the Oe horizon but nutrient concentrations tended to be higher in the Oi horizon. Arthropod abundance was best explained by forest floor mass, while arthropod diversity was best explained by phosphorus, calcium and sodium concentrations in the Oi horizon and by phosphorus concentrations in the Oe horizon. Differences in arthropod community composition between treatments and horizons correlated with phosphorus concentration and dry mass of the forest floor. We conclude that at a local scale, arthropod abundance is related to forest floor mass (habitat space), while arthropod diversity is related to forest floor nutrient concentrations (habitat quality).

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Key words: arthropod community composition; Barro Colorado Nature Monument; habitat quality; litter addition; litter fauna; Oe horizon; Oi horizon.

AN ESTIMATED THREE QUARTERS of the total animal biomass of a tropical rain forest is comprised of small, soil- and litter-dwelling arthropods (Wilson 1990). Soil and litter fauna contribute greatly to decomposition dynamics (Janzen 1987, Coûteaux *et al.* 1995) and nutrient mineralization (Swift *et al.* 1979, Andersen & Swift 1983), and the importance of soil fauna to decomposition and nutrient dynamics is thought to be disproportionately higher in tropical than temperate forests (Heneghan *et al.* 1999, González & Seastedt 2001, Yang *et al.* 2007), because the activity of soil and litter organisms is not greatly constrained by climate variability (Lavelle *et al.* 1993). In addition, soil and litter arthropods represent an important food resource for other forest animals (Kattan *et al.* 2006).

The forest floor is highly heterogeneous over short distances (Milton & Kaspari 2007) and small-scale changes in the chemical and physical properties of the forest floor (*e.g.*, depth, microclimate, nutrient concentrations) will exert a range of direct and indirect effects on the fauna it supports. Although relatively few arthropod species feed directly on leaf litter, it is an important substrate for fungi and bacteria (Swift & Anderson 1989), which in turn are a major source of invertebrate nutrition (Killham 1994, Lodge

1996). The forest floor represents a habitat for both predators and prey; litter accumulation provides more structural complexity and creates a habitat for a more diverse range of insects (Bultman & Uetz 1984, Barberena-Arias & Aide 2003). Nevertheless, litter mass alone does not always explain differences in the number of arthropods present at a site, nor will it affect all trophic or taxonomic groups in the same way: microbivores, for example, are likely to be limited by nutrients (Sterner & Elser 2002, Milton & Kaspari 2007), while predators are more likely to respond to prey density and changes in habitat structure (Uetz 1979). The accumulation of organic matter may also have negative effects on arthropod populations; compaction can reduce habitat space and make the forest floor unsuitable for many taxa (Levings & Windsor 1984) and phenolic compounds from decomposing litter could act as a deterrent to arthropods (Sayer 2006).

The nutritional quality of organic matter is key to determining decomposition rates (Enriquez *et al.* 1993) and it has been suggested that the nutrients driving decomposition will also affect the arthropods involved in the decomposition process and their predators (Kaspari *et al.* 2007, Milton & Kaspari 2007). A recent study found strong evidence for phosphorus limitation of forest litter fauna at a landscape scale in lowland tropical forest (McGlynn *et al.* 2007) but a fertilization experiment in disturbed tropical forest showed little effect of nutrient availability on arthropod abundance at smaller scales (Yang *et al.* 2007) and the increased habitat space provided by thicker litter may ultimately be more important in determining arthropod abundance and diversity than nutrient availability (Gill 1969). Experimental and observational studies of the relationships between arthropod abundance and the quantity of

organic matter on the forest floor, with a few notable exceptions (*e.g.*, Burghouts *et al.* 1992, Yang *et al.* 2007), have been limited to temperate forests (*e.g.*, David *et al.* 1991, Reynolds *et al.* 2003). We hypothesized that small-scale differences in both habitat space and habitat quality will be important predictors of arthropod community composition in the forest floor. To test this, we used a large-scale litter manipulation experiment in a lowland tropical semi-evergreen forest to relate forest floor characteristics to arthropod abundance and diversity to determine: (1) whether differences in forest floor mass are related to arthropod abundance and diversity; (2) whether the nutrients thought to limit decomposition also explain differences in arthropod communities in the forest floor; and (3) whether differences in the characteristics of distinct organic horizons are related to arthropod abundance and diversity.

METHODS

SITE DESCRIPTION.—The study was carried out within an ongoing long-term litter manipulation experiment (Sayer *et al.* 2006a, b, 2007). The forest under study is an old growth lowland tropical forest, located on the Gigante Peninsula ($9°06'$ N, $79°54'$ W) of the Barro Colorado Nature Monument in Panama, Central America. Nearby Barro Colorado Island (*ca* 5 km from the study site) receives a mean annual rainfall of 2600 mm and has an average temperature of $27°C$ (Leigh 1999). There is a strong dry season from January to April with a median rainfall of < 100 mm/mo (Leigh & Wright 1990). Fifteen 45×45 m plots were established within a 40 ha area (500×800 m) of old growth forest in 2000. In 2001 all 15 plots were trenched to a depth of 0.5 m to minimize lateral nutrient and water movement via the root/mycorrhizal network; the sides of the trenches were double-lined with plastic and the trenches were backfilled. Starting in January 2003, the litter (including branches ≤ 100 mm diam.) in five plots was raked up once a month, resulting in low, but not entirely absent, litter standing crop (L− plots). The removed litter was immediately spread on five further plots, approximately doubling the monthly litterfall (L+ plots); five plots were left as controls (CT plots).

SAMPLING.—Litter samples were collected at five randomly chosen sampling sites in each of the CT and L+ plots over a 1-wk period in September 2005. An equal number of plots per treatment were sampled on each collection date. At each sampling site, the depth of the forest floor was measured using a rule-marked knife, a PVC tube of 20 cm inner diam. and 12 cm height was placed on the forest floor and the sample inside the tube was separated from the forest floor by cutting along the inside wall of the tube. The organic horizons of the forest floor were defined according to Brady (1990) and collected separately: the litter layer (Oi horizon), defined as freshly fallen leaves in the early stages of decomposition, was removed from the tube by hand, placed in a preweighed, labeled cloth bag and immediately weighed to the nearest 0.1 g. The depth of the fermentation layer (Oe horizon), defined as denser, fragmented but identifiable organic matter in a more advanced stage of decomposition, was then measured and the sample collected as described above; there was no apparent humus layer (Oa horizon) in the study

forest. Immediately upon returning from the field, the samples were transferred to Berlese funnels lined with 4 mm wire mesh and arthropods were extracted for 24 h, by which time the samples had dried out. The forest floor samples from the funnels were then oven-dried to constant weight at $60°C$ to determine water content and finely ground for nutrient analysis. Phosphorus and cation concentrations were determined after acid digestion by radial view inductively coupled plasma–optical emission spectrometry, total nitrogen was determined by complete combustion gas chromatography by Waite Analytical Services, Adelaide, Australia. The pH of the Oi and Oe horizons was determined on dried, ground subsamples in deionized water (1:3 ratio).

All fauna samples were preserved in 70 percent alcohol until identification. The animals were identified under a stereomicroscope following McGavin (2000) and body length was measured to the nearest millimeter. Most animals were grouped to order level, but in some cases higher and lower taxonomic levels were used; holometabolic larvae were combined into one miscellaneous group. The animals collected also included Annelids and Gastropods but as they were only 2 percent of the total we henceforth use only the terms arthropod abundance and arthropod diversity in the interests of succinctness.

DATA ANALYSIS.—Total arthropod abundance (number of individuals), average body length and Simpson's Index of Diversity ($1 - D$) were calculated for each plot and horizon.

Differences in species composition between treatments and horizons and their relation to forest floor characteristics were analyzed with nonmetric multidimensional scaling (NMMDS) using the Soerensen distance measure in PC-ORD 4.1 for Windows (MjM Software, Gleneden Beach, OR, U.S.A.).

Comparisons between treatments and organic horizons were made for arthropod abundance, body length, diversity and for the properties of the organic layers (mass, depth, water and nutrient content). The paired data of the forest floor layers ($N = 10$) were analyzed with Wilcoxon signed-rank tests. Comparisons between treatments ($N = 5$ per treatment) for each organic layer separately were made using Mann–Whitney U tests. We did not apply a correction of α values for multiple tests, as the tests we performed cannot be considered completely independent and a correction would have resulted in a higher probability of Type II errors (Moran 2003, Gotelli & Ellison 2004).

We explored the relationships between forest floor characteristics and total arthropod abundance and diversity in the organic horizons using stepwise linear regression. To avoid data mining, we considered only those predictor variables that differed between treatments or horizons or were important in determining community composition in our NMMDS analysis (litter depth, litter mass, P, Ca, Na and Mg). Of these, litter depth and litter mass were strongly correlated, and as litter mass differed between both treatments and horizons and was an important predictor in the NMMDS analysis, we excluded litter depth. We thus considered five predictor variables with a sample size of $N = 10$ each; variables were chosen using the stepwise procedure with $P < 0.05$ to enter or $P > 0.1$ to remove (Sokal & Rohlf 1995). All statistical analyses

except NMMDS were performed in SPSS 13.0 for Macintosh (SPSS Inc., Chicago, IL, U.S.A.).

RESULTS

FOREST FLOOR CHARACTERISTICS.—Forest floor depth was 72 percent greater in the L+ plots (38 mm) than the CT plots (22 mm; P = 0.028) but the depth of the individual organic layers did not differ between treatments. Forest floor mass was 65 percent greater in the L+ plots (2148 g/m^2) than the controls (1301 g/m^2; P = 0.047) and the mass of the Oi and Oe horizons were 51 and 68 percent greater in the L+ plots compared with the controls (P = 0.047 and 0.076, respectively; Table 1). Depth was strongly correlated with mass for the forest floor and Oe horizon but not for the Oi horizon. There were no treatment differences in water content, pH or nutrient concentrations of the organic horizons (Table 1).

Over all plots (N = 10), the organic horizons differed from each other in several characteristics; the mass of the Oi horizon (970 g/m^2) was less than the mass of the Oe horizon (2946 g/m^2; P = 0.005) and the water content of the Oi horizon (69.6%) was greater than the Oe horizon (60.7%; P = 0.005), while the concentrations of Ca, Mg, Na and K were higher in the Oi than the Oe horizon (P = 0.041, 0.008, 0.007 and 0.005, respectively).

LITTER FAUNA.—A total of 2077 individuals were identified; 20 groups were identified to order, 2 groups to class, and 1 group to subphylum. Hymenoptera was the order with the most individuals (32 percent of the total number of individuals collected), 99 percent of which were ants. Acarina was the second most abundant order (14 percent of all individuals collected), and larvae made up 11 percent of all individuals collected.

The mean number of arthropods per plot was higher in the L+ plots (274 individuals) compared with the controls (141 individuals; P = 0.047), and the number of individuals in the Oe horizon was also greater in the L+ plots than the controls (P = 0.032) but arthropod body length and Simpson's Index of Biodiversity did not differ between treatments (Table 2).

NMMDS showed clear differences in arthropod community composition between treatments (Fig. 1) and these differences were related to forest floor depth and phosphorus concentration. A two-dimensional solution was sufficient to achieve low stress values and the correlations between arthropod groups and axes showed that Arachnida, Acari and larvae contributed most to the first axis, while Isoptera and Diptera contributed most to the second axis. Of these, Arachnida and larvae tended to be more abundant in the L+ plots (Table 3), while the number of Isoptera in the CT plots was 27 times higher than in the litter addition treatment (Table 3) but their distribution was very patchy.

The Oi and Oe organic horizons differed from each other with respect to arthropod community composition (Fig. 1) but not abundance. A total of 1172 individuals were collected from the Oi horizon and 905 individuals were collected in the Oe horizon. Over all plots, arthropod density was greater in the Oi horizon compared with the Oe horizon (P = 0.005; Table 2) but arthropod diversity and body length were greater in the Oe horizon (P = 0.005 and 0.007, respectively). Coleoptera and Diplopoda tended to be more abundant in the Oe than the Oi horizon (Table 3), while Diptera and Hymenoptera were found in greater numbers in the Oi horizon (Table 3).

RELATIONSHIPS BETWEEN ARTHROPODS AND FOREST FLOOR CHARACTERISTICS.—Multiple regression analysis showed that no combination of the forest floor characteristics that differed between organic horizons or treatments could adequately explain arthropod abundance in the Oi horizon. However, the diversity of arthropods in the Oi horizon was best explained by the model including phosphorus, calcium and sodium concentrations (R^2 = 0.649, P = 0.025), of which calcium concentration was the most important explanatory variable. The abundance of arthropods in the Oe horizon was best explained by a model including dry mass of the Oe horizon, magnesium and sodium concentrations, which accounted for 69.8 percent of the variance (P = 0.016) and the mass of the Oe horizon was the most important explanatory variable in the model. Arthropod diversity in the Oe horizon was best explained by phosphorus concentration and dry mass; the total variance explained by the model

TABLE 1. *Characteristics of the Oe and Oi organic horizons of the forest floor in control plots and litter addition treatments in a lowland tropical forest in Panama, Central America; numbers in parentheses are SE of means for* N = 5.

	Control		Litter addition	
	Oi	Oe	Oi	Oe
Dry mass (g/m^2)	194 ($\pm$ 24)	1107 ($\pm$ 214)	294 ($\pm$ 25)	1854 ($\pm$ 301)
Depth (mm)	11 ($\pm$ 2.6)	11 ($\pm$ 1.5)	15 ($\pm$ 2.0)	23 ($\pm$ 5.7)
Water content (% fresh weight)	68.2 ($\pm$ 1.21)	62.5 ($\pm$ 1.15)	70.9 ($\pm$ 1.09)	58.9 ($\pm$ 2.18)
N (% dry weight)	1.4 ($\pm$ 0.10)	1.4 ($\pm$ 0.09)	1.6 ($\pm$ 0.05)	1.3 ($\pm$ 0.03)
P (mg/kg)	406 ($\pm$ 29.9)	458 ($\pm$ 19.3)	446 ($\pm$ 32.3)	452 ($\pm$ 14.6)
K (mg/kg)	1462 ($\pm$ 235)	696 ($\pm$ 39.7)	1696 ($\pm$ 242)	664 ($\pm$ 60.1)
Ca (mg/kg)	17,300 ($\pm$ 1307)	16,060 ($\pm$ 2516)	17,400 ($\pm$ 943)	11,880 ($\pm$ 424)
Mg (mg/kg)	3040 ($\pm$ 322)	2188 ($\pm$ 143)	3100 ($\pm$ 241)	1926 ($\pm$ 34.8)
Na (mg/kg)	115 ($\pm$ 17.2)	88.7 ($\pm$ 3.13)	134 ($\pm$ 19.2)	80.6 ($\pm$ 11.5)

TABLE 2. *Mean arthropod abundance (number of individuals), density (individuals per gram organic matter), Simpson's Index of Diversity, and size (body length) in the Oi and Oe organic horizons in control plots and litter addition treatments in a lowland tropical forest in Panama, Central America; numbers in parentheses are SE of means for N = 5; different upper case superscript letters within a row indicate significant differences between treatments and lower case superscript letters indicate significant differences between horizons within a treatment at* P < 0.05.

	Control		Litter addition	
	Oi	Oe	Oi	Oe
Abundance (No. ind./m^2)	1360 ($\pm$ 242)	899 ($\pm$ 94)[A]	2384 ($\pm$ 658)	1993 ($\pm$ 416)[B]
Density (No. ind./g)	6.98 ($\pm$ 0.7)[a]	0.93 ($\pm$ 0.19)[b]	9.36 ($\pm$ 3.3)[a]	1.08 ($\pm$ 0.19)[b]
Simpson's Index of Diversity (1 $-$ D)	0.69 ($\pm$ 0.06)[a]	0.80 ($\pm$ 0.01)[b]	0.73 ($\pm$ 0.03)[a]	0.79 ($\pm$ 0.02)[b]
Body length (mm)	2.17 ($\pm$ 0.13)[a]	3.14 ($\pm$ 0.17)[b]	2.41 ($\pm$ 0.13)	2.96 ($\pm$ 0.15)

was 47.6 percent (*P* = 0.043), but phosphorus concentration alone explained 42.6 percent (*P* = 0.024).

DISCUSSION

The depth and mass of the forest floor was increased by our litter addition treatments, but pH, water content and nutrient concentrations remained unaffected. Thus, the litter addition treatment allowed us to study arthropod communities over a wide range of forest floor depths without affecting forest floor nutrient concentrations.

The number of arthropods collected in this study probably underestimates the actual number of arthropods in the forest floor for two reasons: firstly, the size of the sampling frames used (0.0625 m^2) likely excluded many larger arthropods and resulted in low abundances of, for example, millipedes, centipedes and large beetles; secondly, sampling efficiency of Berlese traps varies greatly between arthropod groups, with low sampling efficiency (< 50 per-
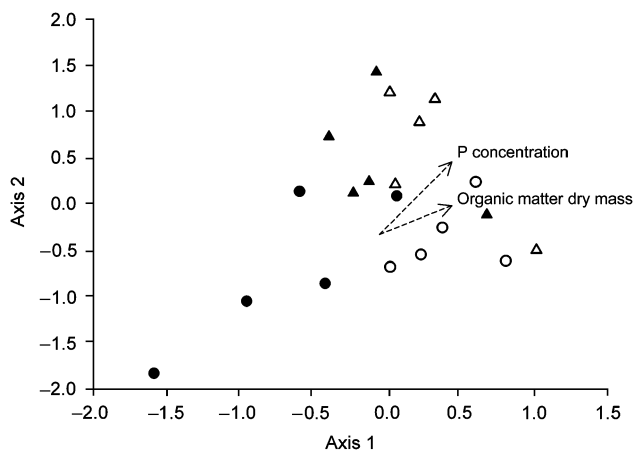

FIGURE 1. Nonmetric multidimensional scaling plot based on the Soerensen distances in arthropod community composition between control plots (circles) and litter addition plots (triangles) and the Oi horizon (closed symbols) and Oe horizon (open symbols) in a lowland tropical forest in Panama, Central America; arrows show the forest floor characteristics correlated with arthropod community composition.

cent) for Acari, Annelidae, Collembola, Diplura, Diptera and Lepidoptera (Levings & Windsor 1982). Nevertheless, Acari, Collembola and Diptera were abundant in our samples and the relative values are reliable for comparing treatments and horizons in this study. Our identification to order level was considered sufficient, as assemblage differences at higher levels have been shown to reliably reflect those at species levels (Williams & Gaston 1994, Balmford *et al.* 1996).

The greater abundance of arthropods in the L+ plots can be attributed to the greater mass and depth of the organic horizons in this treatment, as nutrient concentrations, water content and pH did not differ from the controls. There were no differences between treatments when arthropod abundance was calculated as number of individuals per unit litter mass (Table 2), rather than unit area, which is a further indication that the treatment differences were solely due to differences in the mass of organic matter. Studies in tropical forests in Malaysia and Puerto Rico have shown that an increase in litter quantity may be more important than an increase in litter quality in determining arthropod abundance (Burghouts *et al.* 1992, Yang *et al.* 2007) because the increased structural complexity with greater litter depth provides more habitat space (Uetz 1979, Barberena-Arias & Aide 2003) and a greater number of refuges from predators (Pearse 1943). Other studies in tropical forests have found no strong relationship between arthropod numbers and litter mass or depth, but this can be attributed to seasonal differences or sampling methods. For example, arthropod abundance is poorly related to litter mass during the dry season, when litterfall is high but arthropod abundance low due to lack of moisture (Levings & Windsor 1982, 1984) and the number of arthropods caught in pitfall traps does not always correlate well with litter depth (McGlynn *et al.* 2007) as the deeper the litter around the trap, the greater the structural complexity and the less litter animals are likely to walk into pitfall traps (Greenslade 1964).

Although it is conceivable that soil fauna is transferred with the litter to the L+ plots in our study, it is unlikely that the numbers of animals added to the L+ plots with the litter each month has any great bearing on our results. The monthly accumulation of litter in the L− plots between raking events at the time of the study was low (2.2 g/m^2/d; E. J. Sayer & E. V. J. Tanner, unpubl. data) and the sparse litter cover in combination with repeated disturbance in

TABLE 3. *Total numbers of arthropods in samples taken from the Oi and Oe horizons of control and litter addition plots in a lowland tropical forest in Panama, Central America.*

Taxa	Control			Litter addition		
	Oi	Oe	Total	Oi	Oe	Total
Annelida	10	7	17	4	15	19
Arachnida	70	53	123	145	118	263
Araneae	20	8	28	15	17	32
Acarina	45	40	85	93	87	180
Opiliones	0	0	0	2	1	3
Pseudoscorpionida	5	5	10	35	13	48
Collembola	24	9	33	38	38	76
Entomobridae	2	1	3	0	0	0
Isotomidae	9	2	11	22	21	43
Onychiuridae	6	5	11	14	14	28
Smithinuridae	7	1	8	2	3	5
Crustacea	6	5	11	14	22	36
Isopoda	6	5	11	14	22	36
Entognatha	2	7	9	1	20	21
Protura	0	0	0	0	2	2
Diplura	2	7	9	1	18	19
Gastropoda	2	8	10	1	3	4
Insecta	273	124	397	463	272	735
Orthoptera	3	1	4	2	4	6
Blattaria	1	4	5	5	2	7
Coleoptera	18	28	46	26	61	87
Staphilinidae	1	0	1	2	0	1
Diptera	45	23	68	35	13	48
Hemiptera	8	1	9	6	9	15
Hymenoptera	40	60	100	384	182	566
Isoptera	157	5	162	5	1	6
Lepidoptera	1	2	3	0	0	0
Myriapoda	6	16	22	18	50	68
Diplopoda	6	16	22	18	45	63
Chilopoda	0	0	0	0	5	5
Symphyla	0	0	0	1	4	5
Symphylan	0	0	0	1	4	5
Holometab. larvae	32	53	85	62	81	143
Total	425	282	707	747	623	1370

the L− plots is not likely to invite colonization by a sizable community of litter fauna, especially of larger animals. In addition, more mobile animals are liable to abandon the litter during litter raking and transport. While it is possible that smaller arthropods such as Collembola and Acari are added to the L+ plots with the litter, a previous study using litter bags showed that the abundance of mesoarthropods in the L− plots is greatly reduced (Sayer *et al.* 2006b). Thus the numbers of animals added with the litter is expected to be small compared with the overall effect of accumulated litter after 3 yr of litter addition treatments.

We had predicted reduced numbers of arthropods in the Oe horizon due to greater compaction of the organic matter and lower nutrient levels. Contrary to expectations, arthropod abundance did not differ between organic horizons and the body size of arthropods was greater in the Oe than in the Oi horizon. Arthropod abundance was not related to the compactness (calculated as dry weight per 1 mm depth) of either of the organic horizons and the greater mass of the Oe horizon probably provided more habitat space for larger arthropods such as Coleoptera and Diplopoda, which were more abundant in this horizon.

The greater forest floor mass in the L+ plots did not affect any one particular trophic group; we found higher numbers of detritivores (*e.g.*, Diplopoda), microbivores (*e.g.*, Collembola) and predators (*e.g.*, Arachnida, in particular Pseudoscorpionida) in the L+ plots. Detritivores and microbivores are likely to be attracted to the greater resource availability in patches with greater forest floor mass, while predators are more likely to respond to the greater availability of prey in thicker litter (Uetz 1979, Chen & Wise 1999, Milton & Kaspari 2007); this is demonstrated in our study by the concurrent increase in abundance of both Collembola and Pseudoscorpions, which are known predators of Collembola (Chen & Wise 1999), in the L+ plots.

The quality of forest floor organic matter played a lesser role in determining arthropod abundance than did forest floor mass but nutrient concentrations were important in explaining differences in diversity. Phosphorus was an important factor in explaining arthropod diversity in both organic horizons and NMMDS analysis demonstrated that phosphorus concentration was strongly related to arthropod community composition. Phosphorus is thought to be the main limiting nutrient for decomposition in the study area (Kaspari *et al.* 2007), as concentrations in the soil are low (Cavelier 1992, Sayer *et al.* 2006a), and decomposition studies have shown net accumulation of phosphorus in the early stages of decomposition (Sayer *et al.* 2006b). A fertilization experiment in the study forest showed that phosphorus stimulated the growth of cellulose-decomposing microbes resulting in greater microbivore biomass in phosphorus fertilized plots (Kaspari *et al.* 2007) and phosphorus was also shown to limit litter fauna at the landscape scale in tropical rain forest in Costa Rica (McGlynn *et al.* 2007).

Despite the high calcium concentrations in the soil and litter in the study forest (Cavelier 1992), small-scale differences in calcium concentrations remained important in explaining the diversity of arthropods in the Oi horizon as many arthropods utilize large amounts of calcium in their exoskeletons (Cromack *et al.* 1977).

We expected the abundance of fungal-feeding arthropods to correlate with potassium concentrations as fungi actively accumulate potassium during the decomposition process and greater potassium concentrations in the litter can be associated with higher fungal biomass (Sayer *et al.* 2006b). In contrast, we found no relationship between potassium concentrations and the abundance or diversity of arthropods in this study, even though potassium is also thought to limit decomposition in this forest (Kaspari *et al.* 2007).

Higher sodium concentrations were related to the abundance of arthropods in the Oe horizon and the diversity of arthropods in the Oi horizon. Sodium is a highly mobile nutrient but many decomposer fungi accumulate sodium in their fruiting bodies, which may attract litter arthropods (Schowalter 2006). Numerous invertebrates have high assimilation rates for sodium (Reichle *et al.*

1969) and arthropod tissues can contain concentrations of sodium that are much higher than those found in leaves or litter (Cromack *et al.* 1977). Thus, sodium may be a limiting nutrient for some arthropod groups in the study forest.

CONCLUSIONS

Our results demonstrate that, on a local scale, differences in the numbers of arthropods in the forest floor can be explained mostly by variation in the mass of the organic horizons, which suggests that available habitat space is the most important predictor of arthropod abundance. In contrast, arthropod diversity was strongly related to small-scale differences in the concentrations of phosphorus, sodium and calcium, suggesting that habitat quality is more important in maintaining diversity. Thus, local-scale differences in arthropod community composition are explained by the influence of habitat space on the number of individuals and the influence of habitat quality on taxonomic diversity.

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