Litter manipulation and the soil arthropod community in a lowland tropical rainforest

O.S. Ashford [a],[*], W.A. Foster [a], B.L. Turner [c], E.J. Sayer [d], L. Sutcliffe [a], E.V.J. Tanner [b]

[a] Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
[b] Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB2 3EA, UK
[c] Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancon, Panama
[d] Department of Environment Earth and Ecosystems, The Open University, Walton Hall, Milton Keynes MK7 6AA, UK

ARTICLE INFO

ABSTRACT

Tropical soil arthropod communities are highly diverse and provide a number of important ecosystem services, including the maintenance of soil structure, regulation of hydrological processes, nutrient cycling and decomposition. Experiments in temperate regions suggest that litter dynamics are important in determining the abundance, richness and community composition of soil fauna, but there is little information for lowland tropical forests. We used a long-term litter manipulation experiment (removing, doubling and control) in a neotropical forest to investigate the consequences of changing litter dynamics on the soil arthropod community. The abundance and biomass of arthropods were reduced significantly by the removal of litter, but not affected by litter addition. Litter manipulation had no effect on simple measures of taxonomic richness or diversity, but multivariate ordination techniques revealed a significant shift in arthropod community composition with the removal, but not addition, of litter. This suggests the overall importance of top-down controls on the arthropod community in this ecosystem, with bottom-up influences only important following the removal of large quantities of litter. Of the parameters measured, the faunal composition of experimental plots was best predicted by litter depth and the concentrations of total carbon and readily-exchangeable phosphorus (in order of importance), highlighting the influential role of soil chemical properties, in addition to the physical properties of litter, in shaping soil arthropod communities. Comparison with the results of a previous study of litter-dwelling fauna in the same litter manipulation experiment suggested that the soil and litter arthropod communities are influenced by different parameters: total carbon and litter depth for the soil community, but sodium and calcium for the litter community, although phosphorus was important in both environments. We conclude that arthropod community composition is controlled by different factors in the soil than in the litter and is affected by decreasing, but not increasing, depth of litter.

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1. Introduction

Estimates of the total number of extant species on Earth range from 3.6 million to over 30 million (Wilson, 2002; Hamilton et al., 2010). Many of these species are terrestrial arthropods that live in the soil for at least part of their life cycle (Giller, 1996). In fact, soil communities are thought to be amongst the most species rich components of terrestrial ecosystems (Anderson, 1975). For instance, the volume of soil beneath 1 m^2 of temperate beech woodland can contain more than 1000 species of soil animals (Anderson, 1975). Tropical soil communities are likely to be even more species rich; being home to possibly twice as many species as occur in rainforest canopies (Ruiz et al., 2008). Indeed, mature forest soils appear to have a taxonomic diversity greater than any other habitat on Earth except coral reefs (Behan-Pelletier and Bisset, 1992), perhaps as a result of the wide array of microhabitats that soil provides (Coleman, 2001; Bardgett, 2002).

These diverse soil communities provide a number of important ecosystem services; for example, soil arthropods maintain soil structure, regulate the porosity of soil, and hence influence hydrological processes and aeration (Lavelle, 1996; Ruiz et al., 2008). They also play a key role in ecosystem carbon dynamics, with a positive relationship between species richness and rates of carbon cycling, which is of significance since approximately 80% of global terrestrial carbon is stored in soils (Nielsen et al., 2011).

Furthermore, the soil fauna is a key component of ecosystem nutrient cycling, influencing the availability of nutrients both for soil-dwelling organisms and for plants (Giller, 1996; Lavelle, 1996; De Deyn et al., 2004; Ruiz et al., 2008).

Despite the importance of soil organisms in ecosystem functioning, factors governing their ecology remain poorly understood. Current information indicates soil organisms to be partially dependent on inputs of detrital material from photosynthetic organisms (a substantial part of which is composed of plant material, such as leaves, woody debris, fruit and flowers; henceforth referred to as 'litter'), and this forms the basis for the present study.

Organic matter inputs to the soil, including leaf litter, root litter and root exudates, represent the energy base of the soil food web and are directly utilised by aerobic and anaerobic bacteria, fungi, and a variety of arthropods (Verhoef and Brussaard, 1990; Lavelle, 1996). Important arthropod functional groups include the 'litter transformers' and the 'ecosystem engineers'. Litter transformers comprise arthropods of the mesofauna (<2 mm in length) such as Collembola (Verhoef and Brussaard, 1990), as well as macrofauna (>2 mm in length) such as Isopods (Ruiz et al., 2008). Litter transformers consume the litter (including its associated microbial community), which rapidly passes through their digestive tract, producing faecal pellets. These pellets act as incubators for microbial activity and are re-ingested by the litter transformers some time after deposition, so that metabolites released by microbial action can be assimilated (Lavelle, 1996).

Ecosystem engineers comprise those organisms that are able to effectively move through the soil, like Isoptera and Oligochaeta (Lavelle, 1996; Ruiz et al., 2008). Such organisms physically modify, maintain and create habitats for other members of the community (Ruiz et al., 2008) and in doing so decrease soil density, mix soil horizons and improve aggregate structure (Knoepp et al., 2000). They are often large (generally 5−100 mm) and can develop symbiotic relationships with microorganisms in their digestive tract, enabling them to feed directly on litter. In terms of predacious groups, bacteria and fungi can be consumed directly by micropredators (like nematodes and protozoa; Lavelle, 1996), while significant secondary and tertiary predators include Araneae, Pseudoscorpiones, Chilopoda and some Acari (Wilson, 2002).

Since litter forms a substantial part of the foundation of the soil food web, any process that modifies the rate of litter inputs to the forest floor has the potential to directly influence the soil community. Short-term variation in forest litter dynamics occurs naturally (e.g. over an annual cycle), but longer-term changes can result from anthropogenic perturbations such as climate change (Cao and Woodward, 1998; Zak et al., 2003) and forest fragmentation (Sizer et al., 2000). Litter manipulation experiments are an excellent way to investigate the influence of changes in litterfall on soil-dwelling organisms and previous work has shown litter quantity to be an important factor in determining arthropod abundances (Wardle, 2002). Removal of litter generally leads to a decline in the abundance of soil-dwelling arthropods (Pearse, 1943; Gill, 1969; David et al., 1991; Ober and DeGroote, 2011), whereas the addition of litter leads to a slight increase in soil arthropod abundance (Poser, 1990; David et al., 1991; Arpin et al., 1995), although this is not nearly as pronounced as the effect of litter removal. Litter manipulation can also change the community composition and population dynamics of soil-dwelling arthropods (Ponge et al., 1993; Osler et al., 2006), and shifts in soil fauna have been attributed to the importance of the physical presence of litter (Pearse, 1943; Gill, 1969; Uetz, 1979; Judas, 1990) such as the role of litter as a microclimatic buffer (David et al., 1991) or as a protective barrier from terrestrial predators (Pearse, 1943). Little is currently known concerning the influence of chemical parameters on soil fauna.

It is notable that all the above studies are from temperate ecosystems and there has been little research in tropical forests. A previous manipulative study focussing on litter-dwelling arthropods (Sayer et al., 2010) found that arthropod abundance was best explained by forest floor mass, while arthropod diversity was best explained by phosphorus, calcium and sodium concentrations in the litter horizons. However, to our knowledge, the impact of large-scale litter manipulation upon communities of soil-dwelling arthropods remains largely unknown. To address this, we examined the influence of experimental litter manipulation in a lowland tropical forest in Panama on the soil arthropod community. We measured arthropod abundance, biomass, taxonomic richness, diversity, and community composition, and focussed predominantly on faunal responses to chemical changes in the soil as a result of long-term litter manipulation.

2. Methods

2.1. Site description

Samples were taken from long-term, large-scale litter manipulation plots located on the Gigante Peninsula of Barro Colorado Nature Monument (9°06′N, 79°54′ W), Republic of Panama. Nearby (∼5 km) Barro Colorado Island (BCI) has an annual average temperature of 27 °C. Potential evapotranspiration and average rainfall are 1440 mm and 2600 mm per year, respectively, and 90% of rainfall occurs during a rainy season lasting from May to December (Windsor, 1990). Soils at the study site are moderately acidic (pH 4.8−6.1) Endogleyic Cambisols to Acric Nitrisols (FAO classification; Koehler et al., 2009).

The Gigante Litter Manipulation Project was established in 2000 and consists of 15 plots measuring 45 m × 45 m. All plots were trenched to a depth of 50 cm to minimise transport of nutrients and water by roots and mycorrhizas. The trenches were double-lined with plastic and back-filled. Starting in January 2003, all litter was removed from five plots once a month (L− plots) and immediately spread over five plots (effectively doubling the litter standing crop; L+ plots); five plots were left undisturbed as controls (see Sayer and Tanner, 2010 for a detailed description of the experiment).

2.2. Soil and arthropod sampling

Five sets of three cores (5 cm diameter, 10 cm depth) were taken at equal distances along one transect in each plot during July/August 2010. At each sampling site, the depth of litter was measured and then cleared to expose the mineral soil prior to soil sampling. An equal number of plots per treatment were sampled on each collection date.

Immediately upon returning from the field, soil samples were transferred to Berlese−Tullgren funnels lined with 4 mm wire mesh. Arthropods were extracted for 48 h (by which time the soil samples were dry) and stored in 80% ethanol. Samples were weighed immediately after arthropod extraction.

Since Berlese−Tullgren funnels have been reported to have a relatively low sampling efficiency (<50%) for some taxa including Acari, Oligochaeta, Collembola, Diplura and Diptera (Levings and Windsor, 1982), sub-samples of the soil were examined under a binocular microscope to determine efficacy of arthropod extraction; a near-zero abundance of arthropods remaining in the soil demonstrated that the extraction method was effective.

2.3. Soil analysis

Soil samples for nutrient analysis (0−10 cm depth) were collected from the five marked transect points in each plot in

August 2010 and pooled to give one composite sample per plot. Sub-samples for analysis of inorganic nitrogen were extracted in the field by immediately placing ∼10 g of soil in pre-weighed bottles containing 50 ml of 2 M KCl to minimise changes in nitrogen concentrations due to storage (Worsfold et al., 2005; Turner and Romero, 2009). Samples were centrifuged upon returning to the laboratory (<6 h) and the extracts were frozen prior to analysis for nitrate and ammonium by automated colourimetry using a Lachat Quikchem-8500 (Hach Ltd, Loveland, CO).

Exchangeable cations were determined on fresh soil by extraction in 0.1 M BaCl$_2$ (Hendershot et al., 2008) with detection by inductively coupled plasma-optical emission spectrometry using an Optima 7300DV (Perkin–Elmer, Inc., Shelton, CT). Readily-exchangeable phosphorus was determined by extraction with anion-exchange resins with detection by automated molybate colourimetry using a Lachat QuikChem-8500 (Turner and Romero, 2009). Total carbon and nitrogen were determined on dried and ground samples by combustion and gas chromatography using a Thermo Flash 1112 CN analyser (CE Elantech, Lakewood, NJ). Soil pH was measured on fresh soil in deionised water and 0.01 M CaCl$_2$ (1:2 soil to solution ratio) using a glass electrode.

2.4. Arthropod identification

All individuals were identified to order or better under a stereomicroscope following McGavin (2000) at the Museum of Zoology, University of Cambridge, UK. Identification to order or family was considered sufficient since higher taxonomic levels act as reliable surrogates for patterns of species richness (Balmford et al., 1996a,b; Baldi, 2003). Due to the rare or obscure nature of a number of the families identified, the analysis was based on ordinal level data (see Table 2). The body length of each individual was measured to the nearest 0.1 mm. A reference collection was deposited with G.B. Fairchild at the 'Museo de Invertebrados de la Universidad de Panama'. Previously published data of litter arthropod communities from the same experiment was taken from Sayer et al. (2010) and compared to the soil communities reported in the current paper.

2.5. Statistical analysis

Preliminary analysis showed that one of the control plots had unusually sparse litter cover and was therefore excluded from further analyses. Thus, all analyses were based on plot means with 4 replicates for the controls and 5 replicates for each of the litter addition and removal treatments. Total abundance, arthropod abundance standardised to soil dry mass, individual taxon abundance, arthropod community dry biomass and Simpson's Index of Diversity (1-D) were calculated. Biomass was calculated following length/dry biomass regressions supplied by Schoener (1980) and Richardson (unpublished data; Supplementary material, Table S1). Simpson's Index of Diversity (1-D) was chosen to enable direct comparison of the data with previously published results for litter-dwelling arthropods (Sayer et al., 2010).

Univariate analyses (comparisons of all soil chemical and physical variables and arthropod total abundance, arthropod abundance standardised to soil dry mass, individual taxon abundance (where abundance was greater than 20 individuals), arthropod community dry biomass and Simpson's Index of Diversity (1-D)) were performed using R 2.12.1 (R development Core Team, 2010). All data were tested for normality. Normally distributed data, after transformation if necessary, were analysed using Analysis of Variance (ANOVA), and any significant results were followed by pairwise comparisons of means (Tukey contrasts). Data that were resistant to transformation were analysed using the Kruskal–Wallis test followed by two-sample Wilcoxon tests for multiple comparisons.

Taxa accumulation curves, based on the Mao-Tau procedure of Colwell et al. (2004), were plotted (including 95% confidence intervals) to visualise the relationship between sampling effort and cumulative number of taxa identified for each treatment. Since these curves did not plateau, values of Chao 2 (Chao, 1987) were calculated using EstimateS (Colwell, 2009) to estimate plateau incidence-based taxa richness for each treatment.

Multivariate analyses were performed with Pisces Environmental Community Analysis 2.01 or Pisces Community Analysis Package 3.2 (Seaby et al., 2004a,b). Treatment effects on arthropod community composition were analysed with Non-metric Multi-Dimensional Scaling (NMDS) and Analysis of Similarity (ANOSIM) based on Bray–Curtis dissimilarity. The response of individual arthropod taxa to litter manipulation was visualised using Principal Components Analysis (PCA), while the environmental variables which best explained arthropod responses to the litter manipulation treatment were identified and illustrated using Canonical Correspondence Analysis (CCA). Plot 11, a control, was excluded from the CCA since preliminary analysis revealed it as a major outlier.

Relative proportions of taxa identified in this investigation were compared with those obtained by previous tropical studies (Buskirk and Buskirk, 1976; Leakey and Proctor, 1987; Atkin and Proctor, 1988; Paoletti et al., 1991; Wiwatwitaya and Takeda, 2004; Palacios-Vargas et al., 2007; De Morais et al., 2010) using NMDS based on Bray–Curtis dissimilarity.

3. Results

3.1. Soil and forest floor physical characteristics

Litter was 39% deeper in the L+ plots (39 mm) than the C plots (28 mm; $p < 0.095$), and was 0 mm in L– plots ($p < 0.0001$). Gravimetric soil water content did not differ among treatments (Table 1).

Calcium, magnesium, nitrate, total carbon and total nitrogen concentrations were significantly higher in the L+ plots compared to the L– plots ($p < 0.002$, $p < 0.05$, $p < 0.001$, $p < 0.016$ and $p < 0.019$ respectively; Table 1). Nitrate concentrations in L+ plots were also significantly higher than those of C plots ($p < 0.0015$) whereas manganese concentrations were higher in the L– plots relative to the L+ plots ($p < 0.043$). Soil pH in CaCl$_2$ was significantly higher in the L+ plots compared to the L– plots ($p < 0.02$) but neither treatment differed from the controls. There were no impacts of litter manipulation on the concentrations of any other nutrient.

3.2. Soil fauna

We identified 2496 individuals to 29 taxa (Table 2), with 76% of individuals being assigned to three orders; Acari (35% of individuals), Hymenoptera (29% of individuals), and Collembola (12% of individuals); of the Hymenoptera, 99% of identified individuals were ants. Total proportions of taxa were shown to be representative of tropical lowland forest (Fig. S1).

Arthropod abundance and mean community biomass per plot differed significantly among treatments ($p < 0.003$ and $p < 0.05$, respectively; Table 3). Abundance was greater in C and L+ treatments compared to the L– treatment, but did not differ between C and L+ treatments. Mean community biomass per plot did not differ significantly between L– and C, or L+ and C plots, although there was a trend for lower mean community biomass in L– relative to C plots ($p = 0.073$). There were no effects of litter manipulation on arthropod diversity (Simpson's index).

Table 1
Chemical and physical properties of soil (upper 10 cm) and forest floor in litter manipulation plots in a lowland tropical forest in Panama, Central America. Values are treatment means ± standard errors for $n = 5$ per treatment for litter removal and litter addition and $n = 4$ for the controls. Soil concentrations are given on an oven-dry soil basis. The letter 'A' denotes a significant difference between L− and L+ plots; 'B' denotes a significant difference between L− and C plots; and 'C' denotes a significant difference between C and L+ plots (at $p < 0.05$: see Methods for statistical details). LOD stands for 'limit of detection'.

Environmental variable	Litter removal	Control	Litter addition	Significance
Litter depth (mm)	0	28 ± 2.6	39 ± 4.9	A B C
Soil water content (%)	35.9 ± 1.2	37.7 ± 0.7	36.5 ± 1.6	
pH (in H_2O)	5.4 ± 0.1	5.7 ± 0.2	5.9 ± 0.1	
pH (in 10 mM $CaCl_2$)	4.6 ± 0.1	5.0 ± 0.2	5.2 ± 0.1	A
Total C (g C kg^{-1})	3.43 ± 0.09	4.01 ± 0.22	4.42 ± 0.19	A
Total N (g N kg^{-1})	0.33 ± 0.01	0.37 ± 0.02	0.40 ± 0.02	A
Extractable nutrients (mg kg^{-1})				
Al	38.8 ± 15.4	12.9 ± 8.2	<LOD	
Ca	891 ± 117 (a	1470 ± 296	2060 ± 134	A
K	50.8 ± 10.7	38.6 ± 3.7	70.7 ± 18.7	
Mg	296 ± 30	422 ± 55	434 ± 32	A
Mn	16.3 ± 3.9	8.3 ± 3.2	4.2 ± 2.1	A
Na	5.4 ± 1.7	5.8 ± 1.7	4.8 ± 2.8	
NH_4	2.41 ± 0.51	2.95 ± 0.39	2.85 ± 0.27	
NO_3	0.08 ± 0.04	0.31 ± 0.09	0.79 ± 0.08	A C
P	0.44 ± 0.06	0.47 ± 0.09	0.55 ± 0.09	

Table 2
Summary of taxa identified in litter manipulation plots in a lowland tropical forest in Panama, Central America. The letter 'A' denotes a significant difference in taxon abundance between L− and L+ plots; 'B' denotes a significant difference in taxon abundance between L− and C plots (at $p < 0.05$: see Methods for statistical details). Only taxa with more than 20 individuals in total across the three treatments were tested for significance.

Taxon		Abundance			Significance
		Litter removal	Control	Litter addition	
Acari		82	320	460	A B
Araneae		6	6	8	
Chilopoda		2	1	12	
Coleoptera		8	36	46	A
	Staphylinidae	1	18	33	A B
	Larvae	4	16	18	
Collembola		58	112	125	
Diplopoda		4	8	15	
Diplura		9	41	44	A B
Diptera		6	24	12	
	Larvae	1	2	2	
Gastropoda		0	1	1	
Hemiptera		7	37	5	
Hymenoptera		1	0	2	
	Formicidae	55	368	300	A B
	Larvae	0	8	1	
Isopoda (sub-order Oniscoidea)		0	2	7	
Isoptera		5	4	18	
Lepidoptera		1	1	0	
Oligochaeta		1	9	11	
Orthoptera		0	1	0	
Pauropoda		2	15	3	
Phthiraptera		0	0	2	
Protura		1	7	0	
Pseudoscorpiones		3	8	1	
Psocoptera		10	22	6	
Solifugae		1	0	2	
Symphyla		7	10	3	
Thysanoptera		2	4	1	
Total		277	1081	1138	
Grand total 2496					

Taxa richness differed only slightly between treatments (Chao2: L+ = 28.0, C = 26.4, L− = 28.5); none of the taxa accumulation curves plotted plateaued (Fig. S2). Acari, Hymenoptera (Formicidae) and Collembola were the three most abundant groups in all three treatments. However, Acari were the most abundant in L+ and L− plots, whereas Hymenoptera (Formicidae) was the most abundant group in control plots.

Of the ten most abundant taxa identified in each treatment, L− and C plots had eight in common, L− and L+ plots had only six in common, and C and L+ plots had seven in common. In both C and L+ plots, the five most abundant groups identified were Acari, Hymenoptera (Formicidae), Collembola, Coleoptera and Diplura.

Principal components analysis (Fig. 1) and univariate analyses (Table 2) showed that litter removal resulted in a significant reduction in the abundance of Acari ($p < 0.01$), Coleoptera (Staphylinidae) ($p < 0.05$), Diplura ($p < 0.001$) and Hymenoptera (Formicidae) ($p < 0.01$) relative to control plots. Litter addition resulted in a significant increase in the abundance of Acari ($p < 0.001$), Coleoptera ($p < 0.05$), Coleoptera (Staphylinidae) ($p < 0.01$), Diplura ($p < 0.01$) and Hymenoptera (Formicidae) ($p < 0.05$) relative to litter removal plots, but such increases were not significant relative to control plots. The abundances of a further eight taxa (Coleoptera larvae, Collembola, Diplopoda, adult Diptera, Hemiptera, Isoptera, Oligochaeta, and Psocoptera), in which there were sufficient individuals to justify statistical analysis (more than 20), did not differ significantly among the litter manipulation treatments.

Beta-diversity was high between L+ and L− plots (mean Bray—Curtis value = 0.660) and between C and L− plots (mean Bray—Curtis value = 0.675), but low between L+ and C plots (mean Bray—Curtis value = 0.284). Of the 19 Bray—Curtis values >0.7 (denoting a high level of beta-diversity between plots), nine were for comparisons of L− and C plots, and 10 were for comparisons of L− and L+. There were no Bray—Curtis values >0.7 for comparisons of C and L+ plots (Table S2).

Clear differences in arthropod community composition resulting from litter manipulation were highlighted by Non-metric Multi-Dimensional Scaling (NMDS). The L− plots were separated from the C and L+ along Axis 1 (Fig. 2). Analysis of Similarity (ANOSIM) showed that the difference in community composition in both C and L+ plots compared to the L− plots was significant (sample statistic (L−/C) = 0.994, $p < 0.008$; sample statistic (L−/L+) = 0.984, $p < 0.004$), whereas the community composition of C and L+ plots did not differ.

A comparison with previously published data of litter arthropod composition in the same plots (Sayer et al., 2010) showed that litter- and soil-dwelling arthropod communities were separated along Axis 2 (Fig. 2). This separation of litter- and soil-dwelling arthropods was statistically significant (ANOSIM sample statistic = 0.672, $p < 0.001$).

3.3. Relation of arthropod responses to soil characteristics

The combination of litter depth and the concentrations of total carbon and readily-exchangeable phosphorus (in order of importance) explained the greatest variance in the biological data (correspondence analysis; Fig. 3). While litter depth and total carbon were particularly important in explaining differences in soil fauna communities among the three litter manipulation treatments, phosphorus concentration did not vary significantly among treatments (Table 1), and instead was important in explaining differences among plots that occurred independently of the litter manipulation treatments. All three variables were positively correlated with increasing arthropod abundance.

Table 3
Summary statistics of soil arthropod communities in litter manipulation plots in a lowland tropical forest in Panama, Central America. Values are mean ± standard errors for $n = 5$ per treatment for litter removal and litter addition and $n = 4$ for the controls. The letter 'A' denotes a significant difference between L− and L+ plots; 'B' denotes a significant difference between L− and C plots (at $p < 0.05$: see Methods for statistical details).

Measure	Litter removal	Control	Litter addition	Significance
Total sampled order richness	24	26	26	N/A
Plateaux order richness (Chao 2)	28.5 ± 2.0	26.4 ± 0.45	28.0 ± 1.1	
Arthropod abundance (individuals per sample)	55.4 ± 7.9	251 ± 36	227 ± 25	A B
Arthropod abundance (individuals kg^{-1} soil)	104 ± 22	508 ± 85	432 ± 59	A B
Arthropod community dry biomass (mg)	20.4 ± 8.2	51.3 ± 12.9	44.9 ± 6.0	A
Simpson's index of diversity (1-D)	0.734 ± 0.016	0.731 ± 0.022	0.759 ± 0.011	

4. Discussion

4.1. Response of soil fauna to litter manipulation

Litter removal reduced the abundance and biomass of soil-dwelling arthropods, whereas litter addition had no significant effect. This is similar to the results of litter manipulation experiments in temperate ecosystems (Pearse, 1943; Gill, 1969; Poser, 1990; David et al., 1991; Arpin et al., 1995; Ober and DeGroote, 2011).

Litter manipulation appeared to have no influence on measures of diversity or taxonomic richness (Table 3), but as in previous temperate studies (Ponge et al., 1993; Osler et al., 2006) litter manipulation changed the arthropod community composition, with differing responses of several taxa to the treatments (Figs. 1 and 2). Thus, simple measures of diversity and taxonomic richness are not informative in this context because they are relatively insensitive to changes in the low abundances of most taxa identified.

Litter removal was associated with a significant reduction in the abundance of some important soil taxa, in particular ants, mites, staphylinid beetles and diplurans (Table 2). Without further identification (to genus in the case of the ants), it is not possible to assign these groups to feeding guilds, but it is clear that the drastic reduction in important ecosystem engineers, such as the ants, will have major, almost certainly negative, effects on soil structure, nutrient cycling and other soil processes (Knoepp et al., 2000). Ants can directly accelerate litter decomposition in tropical soils

(McGlynn and Poirson, 2012) and their movement through the soil physically modifies, maintains and creates habitats for other soil invertebrates (Ruiz et al., 2008), increases soil pore space (reducing soil density), mixes soil horizons (which may aid nutrient cycling), and improves soil aggregate structure (Knoepp et al., 2000). These results indicate that litter removal, by causing a bottom-up perturbation to the ecosystem, has significant effects on the nature of the soil invertebrate community.

In contrast, the addition of litter had little significant effect on the soil invertebrates: some groups (Chilopoda) increased in abundance and some decreased (Pseudoscorpiones and Protura), but their numbers are too small to allow any firm conclusions to be drawn. This suggests that resource availability does not limit arthropod populations in this lowland neotropical forest, which agrees with results obtained in temperate environments (Salamon et al., 2006). Given the importance of top-down processes that has been demonstrated in a tropical plant/herbivore ecosystem in Costa Rica (Letourneau and Dyer, 1998), it is possible that when resource availability is not limiting, tropical invertebrate populations are mediated from the top-down.

In summary, the limited influence of litter addition on the soil invertebrate community suggests that litter quantity is not a limiting resource in this lowland forest, hinting that top-down, not bottom-up, factors may be the more important in structuring soil arthropod populations. Bottom-up effects were demonstrable only with the removal of large quantities of litter, but they did reduce the abundance of several important soil invertebrate taxa, which could have negative consequences for ecosystem health.
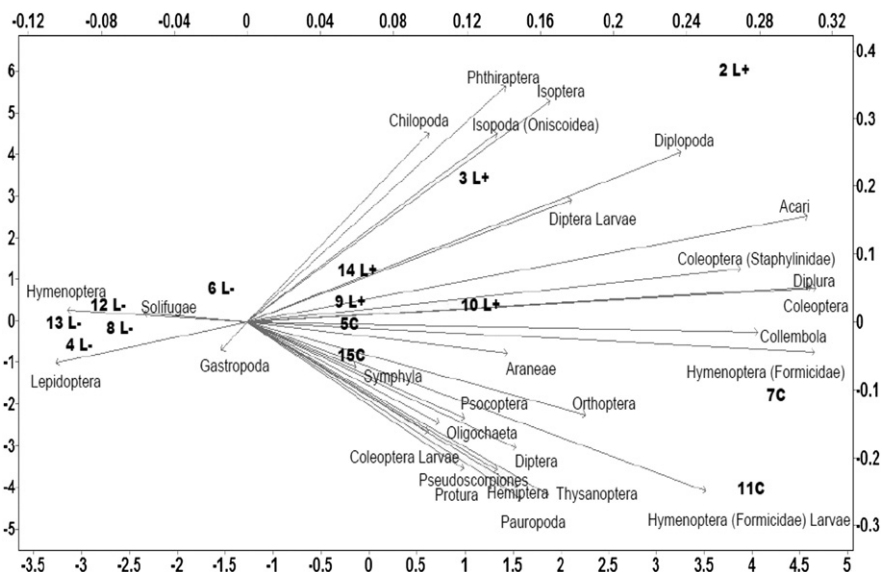

Fig. 1. PCA (correlation) showing the response of individual taxa to litter manipulation treatments in a lowland tropical forest in Panama, Central America. Numbers represent individual plots, while L−/C/L+ refer to litter manipulation treatments ('L−' is litter removal, 'L+' is litter addition and 'C' is controls).
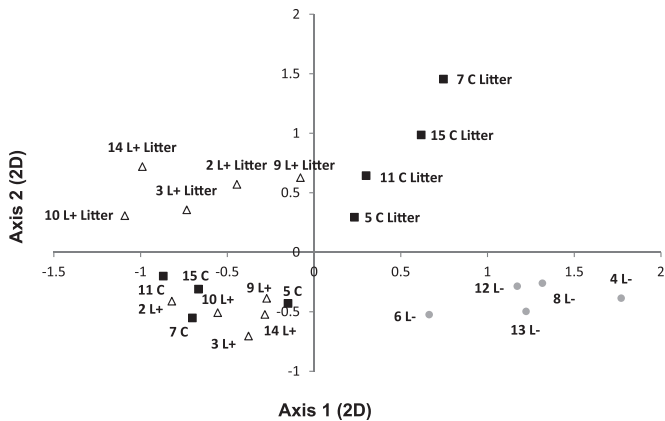
Fig. 2. NMDS plot illustrating the divergence in community composition of soil arthropods (data from current paper) and litter arthropods (data from Sayer et al., 2010; labelled as 'litter') between litter removal plots and control and litter addition plots in a lowland tropical forest in Panama, Central America. Numbers refer to individual plots, while L− (grey circle)/C (black square)/L+ (clear triangle) refers to treatment type ('L−' is litter removal, 'L+' is litter addition and 'C' is controls). The plot was produced using Bray−Curtis as a measure of similarity. Final stress for dimension 1 = 0.269; for dimension 2 = 0.0764.

4.2. Relation of arthropod responses to soil characteristics

The combination of litter depth and the concentrations of total carbon and readily-exchangeable phosphorus (in order of importance) best explained arthropod responses to litter manipulation and differences between individual plots independent of treatment. While total carbon and litter depth were most important in explaining faunal differences among the three litter manipulation treatments, phosphorus concentration was important in explaining faunal differences among plots that occurred independently of the litter manipulation treatment. For example, in Fig. 3, litter depth and total carbon are shown to be important factors in explaining faunal differences between litter removal plots and control and litter addition plots. On the contrary, readily-exchangeable phosphorus concentration is an important factor in explaining faunal differences between plots 6 and 8 (both litter removal plots).

In some litter removal plots (plot 8, for example; see Fig. 3), several elements of fundamental importance to arthropod metabolism became limiting (phosphorus and carbon in particular; Medici and Taylor, 1966; Vigh and Dendinger, 1982; Denno and Fagan, 2003; Capinera, 2008; Schneider et al., 2010). However, no corresponding effects of litter addition were observed in terms of arthropod absolute and relative abundances, which suggests that the above elements were in sufficient supply in most control plots, at least in terms of their effects on soil arthropods.

In contrast to past studies, which have focussed on the significance of physical parameters, our results highlight the important role of soil chemical properties in shaping soil arthropod communities. It therefore appears that the soil fauna responds not only to changes in physical parameters (such as litter depth), but also to multiple components of the soil chemical environment. However, other factors that have not been considered in this study may also drive the responses of the soil fauna to variable litter dynamics; including the importance of leaf litter as a food source (Judas, 1990), as a microclimatic buffer (David et al., 1991) or as a protective barrier against terrestrial predators (Pearse, 1943). These factors were not investigated, but could also play an important role.

4.3. Comparison of soil and litter fauna

Comparison of the present data on the soil community (sampled in month 92 of this experiment) with data on the litter-dwelling community (sampled in month 32 of the same experiment; Sayer et al., 2010) suggests that the litter and soil have distinct arthropod communities and that the effects of the experimental treatments on arthropods are different in the litter layer compared to the surface soil (Fig. 2). While the community composition of litter-dwelling arthropods was significantly altered by litter addition, a corresponding change in the invertebrate fauna was not observed in the underlying soil. Instead, the community composition of the soil fauna was significantly altered only by the complete removal of the litter layer (Fig. 2). Further, Sayer et al. (2010) found that phosphorus, sodium and calcium concentrations explained differences in the community composition of litter-dwelling arthropods, whereas the combination of litter depth and concentrations of total carbon and phosphorus explained differences in soil-
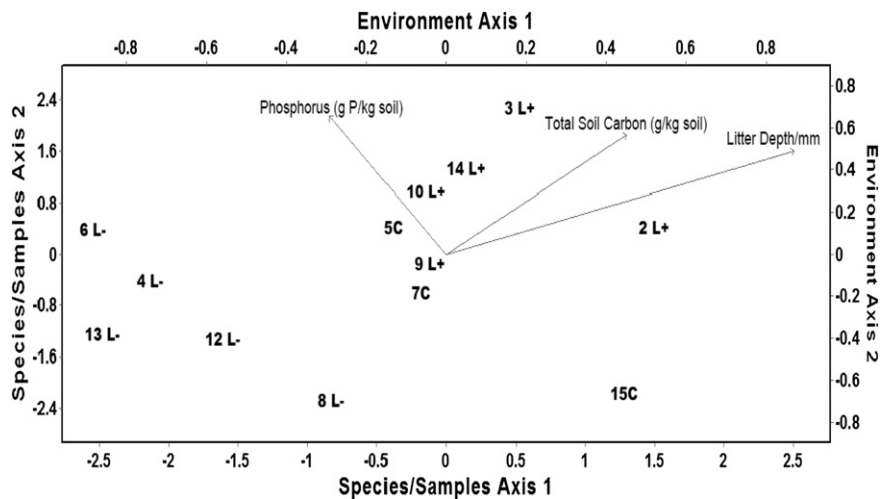

Fig. 3. CCA plot demonstrating the relationship between soil phosphorus concentration, total soil carbon and litter depth and the arthropod community composition in a lowland tropical forest in Panama, Central America. Numbers represent individual plots, while 'L−' is litter removal, 'L+' is litter addition, and 'C' is controls. The relative length of each eigenvector is proportional to the relative importance of each displayed variable in determining the community composition of the experimental plots. The orientation of each eigenvector illustrates the axis of maximum change in the value of each variable across the plot. For example, total soil carbon values are greatest in plots which are towards the upper right of the graph, and are lowest in plots which are towards the lower left of the graph.

dwelling arthropod communities. Hence, although phosphorus concentration appears to be an important predictor for both soil- and litter-dwelling arthropod community composition, these distinct communities are otherwise influenced by different factors. This has also been shown in a previous study on soil arthropods in the temperate zone (Doblas-Miranda et al., 2008).

Our study illustrates the importance of litter inputs for arthropods in the mineral soil, as the reduction in litter inputs to the forest floor reduced the abundance and biomass of the soil fauna and changed the composition of the soil-dwelling arthropod community. In contrast, an increase in litter inputs did not impact the abundance, biomass, taxonomic richness, or community composition of the underlying soil fauna. These findings emphasise the importance of litter dynamics in governing the arthropod community of not only the above ground realm that we are most familiar with, but also the poorly understood and biologically complex subterranean world.

Acknowledgements

Appendix A. Supplementary material

Supplementary material related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2013.03.001.

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