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The effects of litter quantity and quality on soil nutrients and litter invertebrates in the understory of two forests in southern China

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Abstract We designed and carried out a short-term litter decomposition experiment to test the direct effects of litter manipulations on soil nutrients and litter invertebrates in a tropical lowland forest and a diverse subtropical montane evergreen broad-leaved forest in southern China. Our experimental design involved testing both litter quantity and litter quality. To test for the effects of litter quantity, we manipulated different depths of mixed litter, with and without periodic topping-up. To test for the effects of litter quality, we compared four different species of litter individually with mixed, natural, litter control plots. The response by soil nutrients to these manipulations was monitored using ion-exchange membranes and the response by litter invertebrates was estimated using pitfall traps. We show a clear difference in the available soil nutrients and litter invertebrate composition between the two sites. The only response detected in the more diverse montane forests was an invertebrate response to litter quantity. In contrast, we detected both nutrient and invertebrate responses to litter quantity and an invertebrate response to litter species (quality) in the lower diversity forests. We conclude that many of the differences may be attributed to the general temperature and rainfall conditions at the two sites. At the local scale, differences in soil nutrients and invertebrate abundance may partially be explained by litter quantity and the diversity of the forests, and litter abundance has

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a more significant impact on soil nutrients and litter invertebrates than litter species composition.

Keywords Decomposition · Invertebrate diversity · Litter invertebrates · Litter quality · PRS probes · Subtropical montane evergreen broad-leaved forest · Tropical lowland forest

Introduction

Over this last three decades, the study of plant litter decomposition has received much research attention because it is an integral process in ecosystem dynamics, is indicative of site productivity, and influences nutrient cycling and soil fertility (Sylvain and Wall 2011). Plant litter also serves as habitat for communities of organisms such as decomposers, herbivores, and some small mammals. It is extensively documented that decomposition of leaf litter is influenced by environmental conditions, by the identity and abundance of decomposing organisms, and by the chemistry, or quality, of the leaf litter (Heal et al. 1997; Corbeels 2001; Strickland et al. 2009; Sylvain and Wall 2011). At broad regional scales the primary determinants of decomposition rate are temperature and moisture (Aerts 1997; Parton et al. 2007), whereas at finer local scales, various litter quality variables are more important (Hobbie et al. 2006).

These questions mostly focus on the effects of some variable e.g., temperature, moisture, litter quality (Couteaux et al. 1995; Carrillo et al. 2012), litter diversity (King et al. 2002), litter fauna (Barajas-Guzmán and Alvarez-Sánchez 2003), soil fauna (Sylvain and Wall 2011), and various soil characteristics, on rates of litter decomposition and its subsequent effects on nutrient cycling and productivity. This of course is not a linear sequence, rather a complex web (Sylvain and Wall 2011; Ball et al. 2014) with all manner of feedbacks between the components, and as litter decomposes it in turn will influence those factors that have influenced its decomposition—the invertebrate decomposer community (David et al. 1991; Wardle et al. 2006; Sayer et al. 2010), the soil microbial community (Wardle et al. 2006; Strickland et al. 2009; Carrillo et al. 2011), and the nutrient status of the soil (Orwin et al. 2006). The species of tree from which litter is derived can affect decomposition rates and nutrients released from the litter, and this has been shown in both temperate (Hobbie et al. 2006) and tropical (Loranger et al. 2002) environments. Plant litter mixing has been widely studied and but has produced inconclusive results (reviewed by Ball et al. 2014). One argument is that a mixture of different species of litter would provide a more favorable combination of nutrients for decomposers, and attract a wider range of herbivores, and lead to faster breakdown of litter (Hobbie et al. 2006). In addition, it is generally agreed that a more diverse ecosystem will have a lower response to disturbances and stresses than a lower diversity ecosystem i.e., ecosystem properties should be more stable in response to change as diversity increases, although this may not always the case (reviewed by Hooper et al. 2005).

The objective of this study was to investigate two of the direct linkages in the plant litter invertebrate soil system and specifically to test if litter from different species of trees influences the litter invertebrate community and soil nutrient status, and to test if there is any relationship to ecosystem diversity. To achieve this, we chose study sites in a low diversity tropical lowland forest and a high diversity tropical montane forest in southern China. At each site, we manipulated leaf litter abundance and quality by using monospecific litter from four different species, plus mixed natural litter from the site. The response of soil nutrients was monitored using ion-exchange membranes and the response of litter invertebrates was estimated using pitfall traps. We tested the following predictions: (1) the removal of litter will result in a decline in nutrient availability in the soil, and a decrease in litter invertebrates. (2) The addition of litter will result in an increase in nutrient availability in the soil, and an increase in abundance and diversity of invertebrates. (3) Litter mixtures will provide more favorable conditions for decomposers and lead to faster decomposition and higher levels of soil nutrients compared to single species litter. (4) Litter mixtures will attract a more diverse range of invertebrates than single species litter. (5) Responses by soil nutrients and litter invertebrates will be greater in the low diversity lowland forest.

Methods

Study sites

The study was conducted in the forest understory at two sites in Yunnan Province in southern China; the

Xishuangbanna Tropical Botanical Garden (hereafter Xishuangbanna) (21°55′N, 101°15′E; 550 m asl) and close to the Forest Ecosystem Research Station within the Ailaoshan National Nature Reserve (hereafter Ailaoshan) (23°35′–24°44′N, 100°54′–101°30E; 2200 m asl). Xishuangbanna has distinct dry and wet seasons and is classified as tropical lowland forest; mean annual rainfall is 1221 mm (Zheng et al. 2006). Mean annual temperature is 21.7 °C ranging from 14.8 °C in January to 25.3 °C in June (Yang and Chen 2009). The soils are acidic, pH 4.5–5.5 (Cao et al. 2006), and litter is typically 2–3 cm deep (Zhang et al. 2009). Ailaoshan also has distinct wet and dry seasons and is classified as subtropical montane evergreen broad-leaved forest (Young et al. 1992; Qiu et al.1998; Zhu et al. 2006) but because of its higher elevation, it has a more temperate climate than Xishuangbanna; mean annual rainfall is 1931 mm (Liu et al. 2000). Mean annual temperature is 11.3 °C ranging from 5.4 °C in January to 16.4 °C in July. The soils are acidic, pH 4.2–4.9, with a high organic matter and nitrogen content, and litter is typically 3–7 cm deep (Liu et al. 2000). Species richness in the Ailaoshan forest ranges from 68 species per 6 ha (Gong et al. 2011) to 94 species per 0.4 ha (Young and Herwitz 1995). The forests of Xishuangbanna contains over 5000 species of vascular plants (Cao et al. 2006) and 106 species per ha (Lu et al. 2010) but the immediate area of our study is much less diverse with about 30 species of trees.

Experimental design

At each site, three replicate experimental blocks, each approximately 6 m × 6 m, were chosen in flat areas of the understory. At Ailaoshan, the blocks were placed approximately 20 m apart, at Xishuangbanna, due to limitations of flat areas, the blocks were separated by approximately 3 m. Within each block, we removed all loose litter with gentle brushing and marked out 30 plots, each 0.5 m × 0.5 m. We then applied 3 replicates each of 10 different experimental treatments; all treatments were assigned randomly to the 30 plots.

To test the effects of litter quality on soil nutrients and litter invertebrates, we gathered litter from the four most abundant species of trees in the forests and placed the four types of litter in plots at the same depth as the natural litter depth. At Xishuangbanna, those were *Bambusa vulgaris* Schrad ex J.C. Wendl, *Cinnamomum burmannii* (Nees & Th. Nees) Nees ex Blume, *D. retusus* Blume, and *Parashorea chinensis* Wang Hsie. At Ailaoshan, the four species were *Schima noronhae* Reinw. Ex Blume, *Castanopsis wattii* (King ex Hook. F.) A. Camus, *Lithocarpus hancei* (Benth.) Rehder, and *Lithocarpus xylocarpus* (Kurz) Markgr. For the plots that tested the effects of litter species, a loose nylon net (mesh size 4–5 cm) was secured at the four corners of the plot and placed over the litter to prevent it blowing away. All other plots were left uncovered. The control plots had a natural mixture of litter that was removed while clearing the plots; this represented the effect of "naturally occurring" litter.

To test the effects of litter quantity, two different depths of litter (10 and 25 cm) were placed on plots surrounded by a mesh net. In half of these plots, the litter levels were periodically topped up to the original levels as the leaves decomposed, while in the other plots, the litter levels were allowed to decline and were not topped up during the experiment. The litter for these plots was the same natural mixture of litter as used for the control plots. For comparison, the final treatment was bare ground with no litter on the plots. All plots were monitored weekly and new litter (fallen leaves) was removed.

Soil nutrients

We measured soil nutrient availability within each plot throughout the experiment using PRS ion-exchange Probes^{TM} (Plant Root Simulator Probes; Western Ag Innovations, Saskatoon). Each probe has a cation or anion exchange membrane enclosed in a plastic frame. The probes provide an accurate and biologically meaningful measure (Qian and Schoenau 2002) of the availability of 14 different cation and anion elements (NO_3, NH_4, K, Ca, Cl, Na, SO_4, H_2PO_4, Mg, Mn, Cu, Zn, Fe, and Al) although we only used 7 of these for analysis. There were two pairs of anion and cation probes in each 0.5 m × 0.5 m plot. Probes are 15 cm × 3 cm × 0.5 cm with an absorbing surface of 17.5 cm^2. Probes are inserted vertically in the soil so that the absorbing membrane is situated from 6 to 12 cm below ground. Data were pooled to account for within-plot heterogeneity. The first set of probes was inserted in the plots 3 weeks after the initial experimental set up and remained in the soil for 3 weeks. After 3 weeks, the probes were removed, and immediately replaced with new probes, and this was repeated after a further 3 weeks; when the three sets of probes were pooled, this gave a measure of total soil nutrient availability over 9 weeks. Removed probes were washed with deionized water and sent to Western Ag Innovations, Saskatoon, Canada, for analysis.

Invertebrate trapping

We used pitfall traps to sample the litter invertebrate communities. In the center of each 0.5 m × 0.5 m plot, we placed a 250 ml plastic cup countersunk in the ground with the rim of the cup at ground level and covered with a 10 cm × 10 cm piece of plywood elevated at 1 cm above the cup to prevent litter falling into the trap. Each cup was filled to 3 cm deep with a solution of 95 % ethanol for preservation of trapped invertebrates and a small amount of liquid detergent to prevent them from climbing up the walls of the cup. Traps were placed in the ground for 1 week at a time at the beginnings of weeks 1, 4, 7, and 10 for a total of 720 pitfall trap samples. Invertebrate identification was done by the Entomology Section of the Kunming Institute of Zoology and classified to order and/or family.

Statistical analysis

Soil nutrients

Nutrient data were summed through time to provide the total accumulation of each nutrient throughout the 9 weeks of the experiment. An exploratory Principal Components Analysis (PCA) was done to show the relationship of each plot to the correlation pattern among the seven major nutrient variables (Total N,[1] NO_3, NH_4, Ca, Mg, K, and P) in multivariate space. In addition, the difference between treatments was tested using a permutational multivariate analysis of variance (perMANOVA), using Euclidean distances. All multivariate analyses were done using PC-ORD statistical software, version 5.0 (McCune and Mefford 2006).

Using the pooled nutrient accumulation throughout the field season, each nutrient was analyzed independently within each site as follows. Differences between each treatment mean were tested using a one-way analysis of variance (ANOVA) followed by a Tukey's multiple comparison. Five soil nutrients were analyzed—total N, NO_3, Ca, Mg, and K. Phosphorus and NH_4 were initially included, but the levels of these two nutrients were very low, and did not meet either the normality (using the Shapiro–Wilk test) or homogeneity of variances (Levene test) assumptions of ANOVA, and were excluded from further analyses. For graphing purposes, each of the nutrients was presented as a comparison (CI 95 %) between the treatment and the control. The one-way ANOVAs were done using the SPSS statistical package (SPSS Statistics version 20.0 2011).

Litter invertebrates

Invertebrate data were summed over all four sampling periods to reflect their total abundance and taxa richness captured by pitfall traps throughout the experiment (Yang 2004). An exploratory principal components analysis (PCA) was performed to show the relationship of each plot to each of the invertebrate orders in multivariate space. Next, the difference between groups was tested using a permutational multivariate analysis of variance (perMANOVA). Euclidean distances were used in the perMANOVA because a zero value of invertebrates in a trap is meaningful, therefore, the relative nature of Bray-Curtis distances do not apply. All multivariate analyses were performed using PC-ORD statistical software, version 5.0 (McCune and Mefford 2006).

Count data from insect pitfall traps were analyzed by fitting a generalized linear model using the SPSS statistical package (SPSS statistics version 20.0 2011). Invertebrate taxa richness data were fit to a Poisson distribution with a logarithmic link function. To account for overdispersion, the invertebrate abundance data were fit to a negative binomial distribution with a logarithmic link function. Both sets of analyses were done using the log-likelihood ratio Chi-squared test. Invertebrate diversity was calculated using both the Shannon's Diversity Index (*H*) and Shannon's evenness.

Results

Soil nutrients

For both the litter depth (quantity) and litter species (quality) treatments, the two sites show clear

[1] Total N as a sum of NO_3 and NH_4 levels.

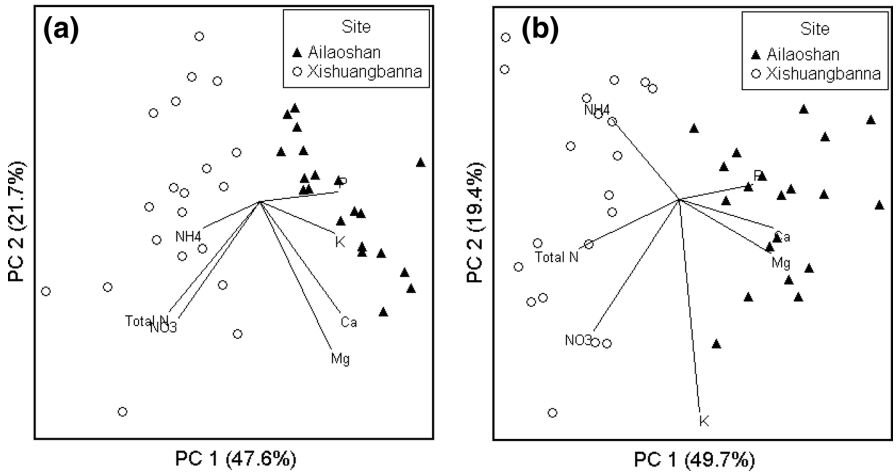

Fig. 1 Ordination of soil nutrients from Xishuangbanna and Ailaoshan plots **a** in response to litter depth treatments and **b** litter species treatments. *Each symbol* represents a single 0.5 m × 0.5 m treatment plot. *Vectors* denote direction and strength of correlations between each nutrient and the PCA axes

significant differences (litter depth, PerMANOVA: $F_{(38,1)} = 26.70$, $p < 0.001$; litter species, PerMANOVA: $F_{(38,1)} = 42.81$, $p < 0.001$) in soil nutrients: Xishuangbanna had higher levels of total nitrogen, nitrate (NO_3), and ammonium (NH_4), while Ailaoshan had higher levels of calcium (Ca), magnesium (Mg), potassium (K), and phosphorus (P) (Fig. 1).

Xishuangbanna

There was a significant ($p < 0.05$) decrease in total N, NO_3, Ca, Mg, and P when litter was removed (Fig. 2a; no litter) compared to the natural litter treatment. Plots with the highest abundance of litter (25 cm of litter with topping) had a significant increase in supply rates of total N, NO_3, Ca, and Mg, but not P (Fig. S1). Other treatments with lesser amounts of litter did not significantly affect the supply rates of the four nutrients, although the general trend was an increase in each nutrient with increasing litter amounts (Table 1). Potassium decreased in all treatments. The responses to different species of litter were extremely variable. There was a general trend of decreasing nutrient availability (Table 1) with only *D. retusus* significantly reducing NO_3 and K, and *B. vulgaris* significantly reducing NO_3 (Fig. 2b).

Ailaoshan

There was a significant ($p < 0.05$) decrease in total N, NO_3, Ca, and Mg when litter was removed (Fig. 2c; no litter) compared to the natural litter treatment. Plots with litter addition treatments mostly had nonsignificant decreases in availability of soil nutrients (Fig. 2c; Table 1). The responses to different species of litter were extremely variable. There were general but nonsignificant trends (Table 1) where most nutrients tended to increase under *L. hancei* and decrease under *S. noronhae* and *L. xylocarpus* (Fig. 2d).

Litter invertebrates

Invertebrate community composition

A total of 8411 invertebrates representing 16 orders were captured: 1850 and 1438, respectively, in Xishuangbanna litter depth and litter species treatments; and 4043 and 1080 in Ailaoshan litter depth and litter species treatments. At both sites, Hymenoptera (bees, wasps and ants) and Diptera (flies) were the most abundant species, with Isoptera (termites) and Araneae (spiders) also common in Xishuangbanna. PCA using the 16 invertebrate orders at the two sites for both the litter depth (Fig. 3a) and litter species (Fig. 3b) treatments show a segregation of plots by site. Hemiptera (cicadas, aphids), Archaeognatha (bristletails), and Dermaptera (earwigs) have a strong association with the Xishuangbanna plots, while Polydesmidae (millipedes), Opilione (harvestman spiders), and Stylommatophora (snails and slugs) have a strong association with the Ailaoshan plots. Hymenoptera (bees, ants) and Isopoda (woodlice, pillbugs) are equally abundant at both sites. Overall, litter depth treatments had a significant effect on the

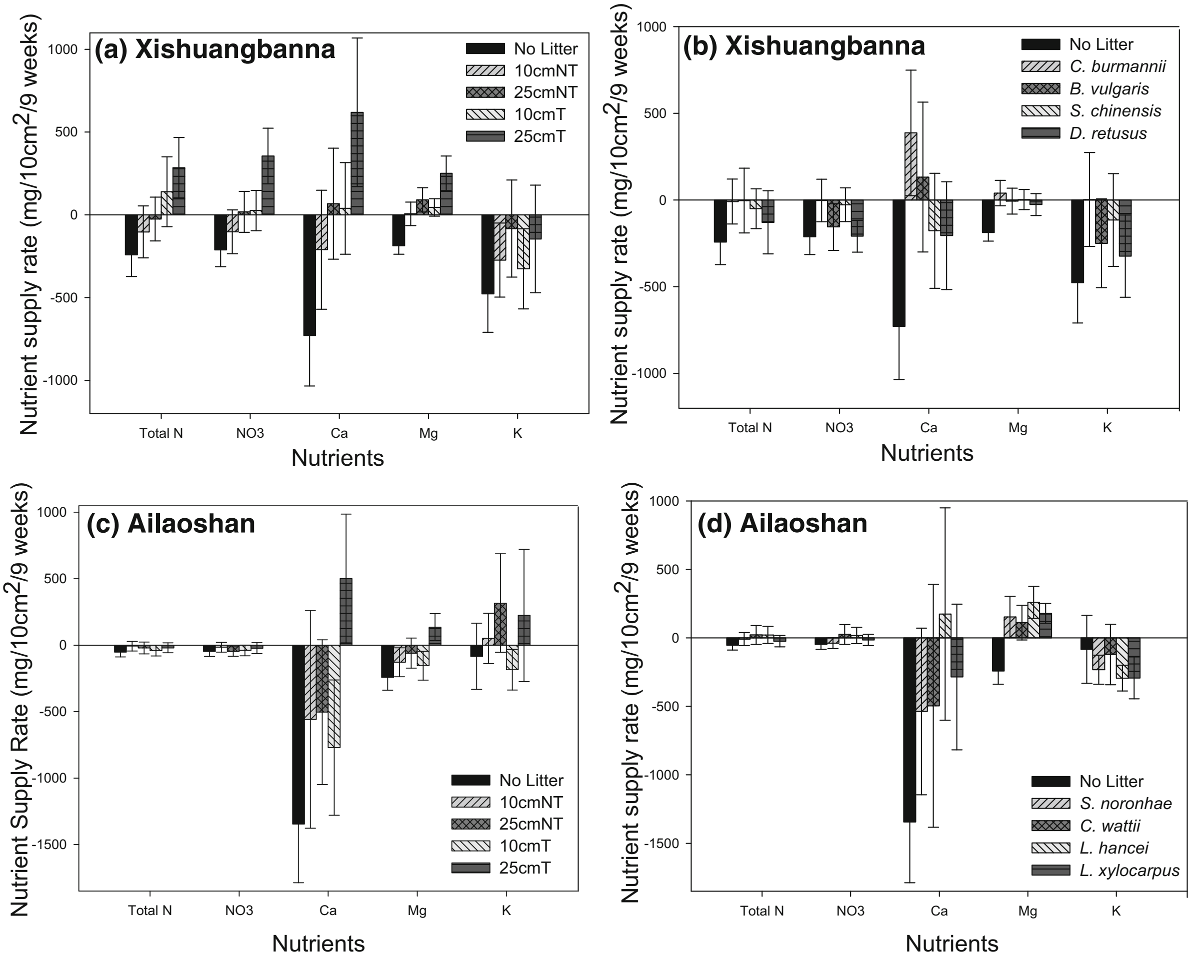

Fig. 2 Mean (±95 % CI) soil nutrients at Xishuangbanna under different **a** litter depth treatments and **b** litter species treatments, and at Ailaoshan under different **c** litter depth treatments and **d** litter species treatments, compared to the control represented by the zero line. *Error bars* that do not overlap the zero line are significantly different from the control. *NT* no topping-up of litter, and *T* topping-up of litter. The species in **b** are *C. burmannii, B. vulgaris, P. chinensis,* and *D. retusus.* The species in **d** are *S. noronhae, C. wattii, L. hancei,* and *L. xylocarpus*

Table 1 Summary of ANOVAs testing for treatment effects of litter depth (quantity) and litter species (quality) on soil nutrients in a tropical lowland forest at Xishuangbanna and a subtropical montane evergreen broad-leaved forest at Ailaoshan

Nutrient	*df*	Xishuangbanna				Ailaoshan			
		Litter quantity		Litter quality		Litter quantity		Litter quality	
		F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Total N	5.18	3.305	**0.027**	1.194	0.351	1.035	0.427	0.746	0.599
NO_3	5.18	6.198	**0.002**	3.335	**0.026**	1.220	0.340	0.870	0.521
Ca	5.18	5.300	**0.004**	3.885	**0.015**	2.670	0.056	1.315	0.302
Mg	5.18	10.725	**<0.001**	5.171	**0.004**	4.491	**0.008**	1.582	0.216
K	5.18	1.728	0.179	2.623	**0.060**	0.670	0.651	1.062	0.412

The sum of squares and mean squares are for between groups

Bold values are significant at $p < 0.05$

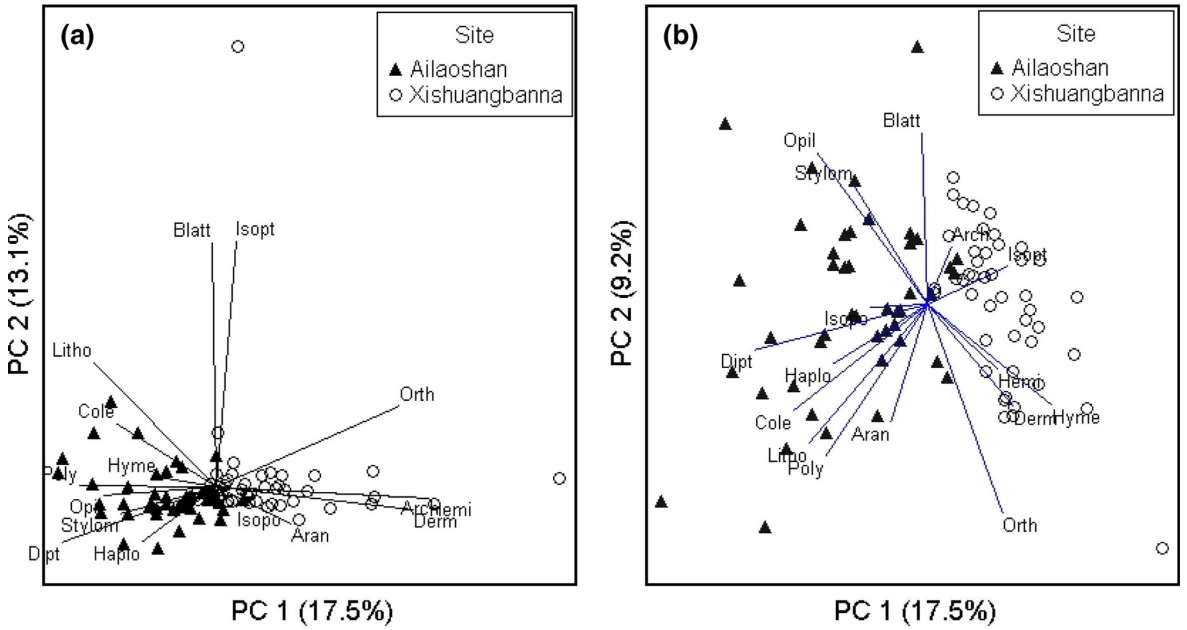

Fig. 3 Ordination of invertebrate communities from Xishuangbanna and Ailaoshan plots, **a** in response to litter depth treatments and **b** litter species treatments. *Each symbol* represents the contents of one pitfall trap. *Vectors* denote direction and strength of correlations between invertebrate orders and the PCA axes

Table 2 Summary of one-way perMANOVA testing for treatment effects of litter depth and litter species on the composition of invertebrate communities

	df	SS	*F*	*p*	Contrasts
Xishuangbanna litter depth					
					[NL, 10NT***]
					[NL, 25NT*]
Treatment	4	10,199	1.9118	**0.0102**	[NL, 25T**]
Residual	40	53,350			
Total	44	63,549			
Xishuangbanna litter species					
Treatment	4	2933.4	1.6902	0.1314	
Residual	40	17,355			
Total	44	20,289			
Ailaoshan litter depth					
					[NL, 25NT*]
					[10NT, 25NT*]
Treatment	4	289,400	2.1871	0.0678	[10T,25NT†]
Residual	40	1,323,200			
Total	44	1,612,600			
Ailaoshan litter species					
					[C, *L. xylocarpus**]
Treatment	4	627.2	1.6204	0.122	[C, *L. hancei*†]
Residual	40	3870.7			
Total	44	4497.9			

Significant pairwise comparisons for each treatment are reported for the contrasts

NL no litter, *10NT* 10 cm no topping-up mixed litter, *10T* 10 cm topping-up mixed litter, *25NT* 25 cm no topping-up mixed litter, *25T* 25 cm topping-up mixed litter, *C* control (natural litter)

Bold values are significant: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; † $p < 0.08$

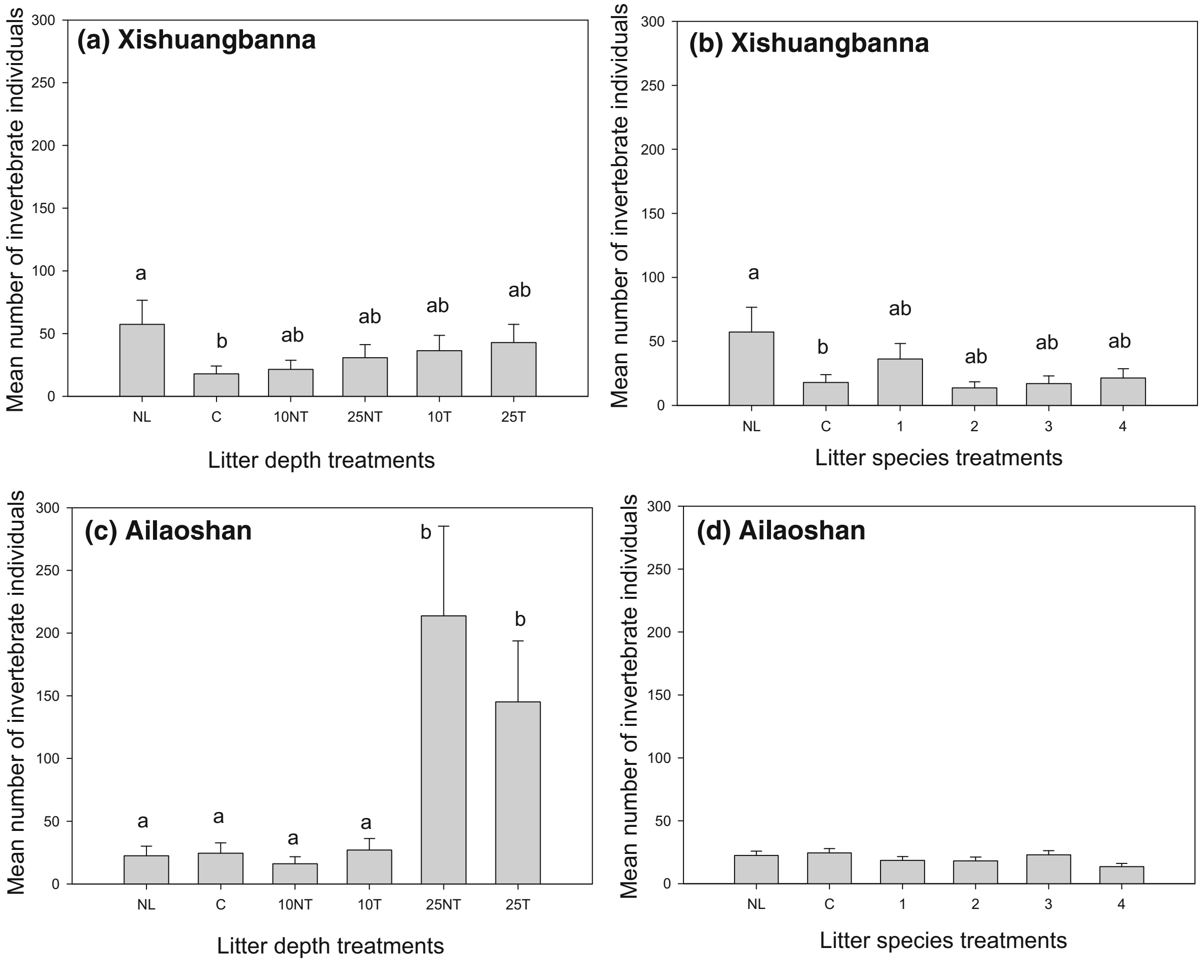

Fig. 4 Mean (+1SE) number of invertebrate individuals caught in pitfall traps at **a**, **b** Xishuangbanna and **c**, **d** Ailaoshan, under different litter depth treatments (**a**, **c**) and litter species treatments (**b**, **d**). Mean values with the *same letters* are not significantly different ($p > 0.05$). *NL* no litter, *C* control (natural litter), *10NT* 10 cm no topping-up of litter, *25NT* 25 cm no topping-up of litter, *10T* 10 cm with topping-up of litter, *25T* 25 cm with topping-up of litter. In **b** the species are 1: *C. burmannii*, 2: *B. vulgaris*, 3: *P. chinensis*, 4: *D. retusus* and in **d** the species are 1: *S. noronhae*, 2: *C. wattii*, 3: *L. hancei*, 4: *L. xylocarpus*

composition of the invertebrate communities at both Xishuangbanna ($p = 0.01$) and Ailaoshan ($p = 0.06$) but litter species treatments had no significant effect at either site (Table 2).

Invertebrate abundance

In Xishuangbanna, both litter quantity (Fig. 4a; $\chi^2_5 = 8.016$, $p = 0.055$) and litter species (Fig. 4b; $\chi^2_5 = 13.773$, $p = 0.017$) treatments had significant effects on invertebrate abundance. In Ailaoshan, litter depth treatments had a significant effect on total invertebrate abundance (Fig. 4c; $\chi^2_5 = 55.96$, $p < 0.001$), with both 25 cm (no topping-up) and 25 cm (with topping-up) having a significantly higher number of invertebrate individuals than any other treatment. Litter species treatments in Ailaoshan had only minor significant effects on invertebrate abundance (Fig. 4d; $\chi^2_5 = 8.670$, $p = 0.123$).

Invertebrate taxa richness

In Xishuangbanna, neither litter depth (Fig. 5a; $\chi^2_5 = 4.146$, $p = 0.529$) nor litter species (Fig. 5b; $\chi^2_5 = 13.773$, $p = 0.017$) had a significant effect on invertebrate taxa richness). In Ailaoshan, litter depth

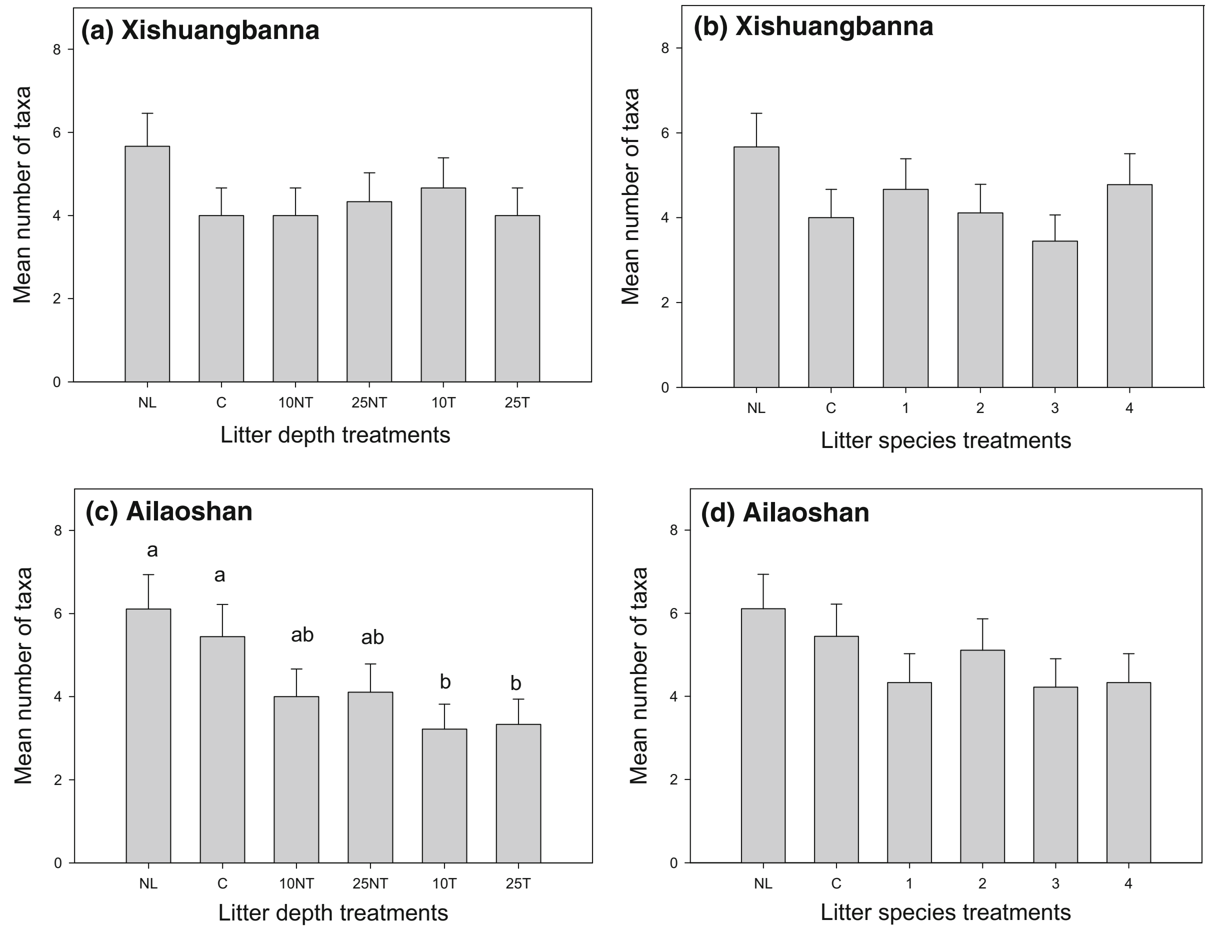

Fig. 5 Mean (+1SE) number of invertebrate taxa caught in pitfall traps at **a**, **b** Xishuangbanna and **c**, **d** Ailaoshan, under different litter depth treatments (**a**, **c**) and litter species treatments (**b**, **d**). In **c**, mean values with the *same letters* are not significantly different ($p > 0.05$); within the three panels **a**, **b**, **d** there are no significant differences in responses. *NL* no litter, **C** control (natural litter), *10NT* 10 cm no topping-up of litter, *25NT* 25 cm no topping-up of litter, *10T* 10 cm with topping-up of litter, *25T* 25 cm with topping-up of litter. In **b** the species are 1: *C. burmannii*, 2: *B. vulgaris*, 3: *P. chinensis*, 4: *D. retusus* and in **d** the species are 1: *S. noronhae*, 2: *C. wattii*, 3: *L. hancei*, 4: *L. xylocarpus*

treatments had a significant effect on invertebrate richness (Fig. 5c; $\chi^2_5 = 13.583$, $p = 0.018$), with both of the topping-up treatments having significantly lower invertebrate taxa richness than the control and the no litter plots. Litter species treatments in Ailaoshan had no significant effect on invertebrate abundance (Fig. 5d; $\chi^2_5 = 5.208$, $p = 0.391$).

Invertebrate diversity

At neither site did the litter depth nor litter species treatments have any significant effect on invertebrate diversity or evenness (Supplementary material, Table S1).

Discussion

Soil nutrients

Soil nutrients at the two experimental sites are distinctly different. Xishuangbanna had higher levels of total nitrogen, nitrate, and ammonium, while the levels of calcium, magnesium, and potassium were higher at Ailaoshan. Phosphorus was equally low in both sites. This result is consistent with previous findings from tropical lowland forests which typically have abundant nitrogen but are limited by phosphorus, while tropical montane forests are more typically limited by nitrogen (Sayer et al. 2012). Some of the differences in nutrient availability from our litter manipulations may be attributed to differences between the montane region of Ailaoshan (>2000 m in elevation) and the lowland region of Xishuangbanna (500 m in elevation). The low pH values of both sites (4.2–4.9 at Ailaoshan, and 4.5–5.5 at Xishuangbanna) are notable, because a low pH indicates that there is a high loss of bases due to leaching, and nutrient levels tend to decrease as pH drops (Tanner et al. 1998). Tropical montane forests have lower net primary productivity and litterfall, and slower decomposition, and plant growth is limited by the reduced nitrogen. The low phosphorus levels in both forests are consistent with previous studies and reviews (Tanner et al. 1998; Sayer et al. 2012), likely due to prolonged leaching and erosion of old weathered soils. Furthermore, a significant proportion of inorganic phosphorus is locked in biologically unavailable components of the soil (Vitousek and Sanford 1986).

Tropical lowland forest at Xishuangbanna

The addition of litter resulted in an increase in soil nitrogen, nitrate, calcium, and magnesium, but potassium decreased in most treatments. Two of the species used are native species in subtropical Asia [*C. burmannii* (Indonesia Cinnamon) and *B. vulgaris*, (Golden Bamboo)] but are able to grow as cultivated stands in other areas of the world, thus have a more generalist growth strategy. The other two species, *P. chinensis* and *D. retusus*, are endemic and highly specialized to the habitats of southern Asia. Taxonomically, these two species are also more closely related to the mixed *Dipterocarpus* leaves used as natural litter for the control. Thus, the significant reduction in nitrate in *D. retusus* treatments compared to the control is surprising. This may have occurred because this field site was dominated by *Dipterocarpus*, consequently, decomposition and changes in soil nutrients may have been amplified due to a home-effect i.e., litter placed beneath the canopy of the same species often decomposes faster because of specialization in the soil biota due to the canopy species (review by Ayres et al. 2009). Our overall result is consistent with our hypothesis that mixtures of litter species provide a more favorable combination for decomposition, as all of the single species of litter showed a decrease in soil nutrients in comparison to the mixed species control.

Subtropical montane evergreen broad-leaved forests at Ailaoshan

The addition of litter had little effect on soil nutrients. This is consistent with Sayer's (2006) review of litter addition experiments where she concluded that increasing litter artificially on a forest floor may not necessarily result in a corresponding increase in soil fauna, fungal, or microbial activity and will simply result in an increased biomass on the forest floor. This is likely more common in higher altitude forests with slower decomposition processes. In our case, the system was much more sensitive to litter removal. Notably this conclusion did not apply to the litter addition plots at Xishuangbanna, probably because the combination of higher temperature and rainfall providing more ideal conditions for rapid decomposition. In previous research near the Ailaoshan site, Liu et al. (2002) investigated litterfall and foliar nutrient concentrations of several dominant species. They used three of the four species we used. They reported that *C. wattii* had high amounts of foliar Ca and foliar N; these foliar measurements did not transfer to our soil measurements. This may be due to the Ailaoshan soils being nitrogen limited, and it is likely that the high nitrogen content originally measured in the leaves may be locked up by the microbial community and not reflected in our PRS probes. However, there may also be a methodological issue. The Liu et al. (2002) result is similar to that reported from other tropical montane forests in Venezuela, Jamaica, and New Guinea. Our contrasting results were obtained using ion-exchange membranes which measures actual nutrient availability to plant roots, while Liu et al. (2002) measured foliar nutrients prior to decomposition, and not the amount of nutrients available to the plants.

Litter invertebrates

Many studies have shown that the exclusion of litter invertebrates leads to drastic reductions in litter breakdown and decomposition rates (Couteaux et al. 1991) and that litter properties strongly influence the diversity and abundance of litter invertebrates (Negrete-Yankelevich et al. 2008; Ball et al. 2014). Experimental studies on the effects of litter on the diversity and abundance of invertebrates have more often involved the removal of litter, and less often on increasing the amount of litter. Sayer (2006) wrote extensively in her review regarding the detrimental effects of litter removal on arthropod abundance and diversity, citing both the direct and indirect loss of litter as food source in trophic interactions of delicate tropical food web relationships. In contrast, studies generally show that with litter addition, there is a slight increase in litter invertebrate abundance and diversity (Arpin et al. 1995), but the effects are minimal compared to the effects of litter removal studies. Indeed, some studies have shown no effect of litter addition on invertebrates (Sayer et al. 2006), and others have shown a negative effect (Uetz 1979). It was not unexpected that the two forest understories differed markedly in litter invertebrate composition because of differences in elevation, temperature, and rainfall (Richardson et al. 2005; Rodriguez-Castaneda et al. 2010). The soils at our two study sites had very different nutrient environments, following the pattern that tropical montane forests are limited by nitrogen, and tropical lowland forests are limited by phosphorus. These soil nutrient differences may underlie major differences in the soil invertebrate community. For example, the availability of phosphorus influences the diversity of arthropods in tropical forests in Panama (Sayer et al. 2010).

Tropical lowland forest at Xishuangbanna

At the Xishuangbanna lowland forest, both the litter addition treatments and litter species treatments had a significant effect on litter invertebrate abundance. This supports our prediction that more litter provides more structural complexity and will attract more invertebrates. Another explanation that cannot be ruled out is that the application of the treatments, i.e., the addition of increasing litter was simultaneously adding increasing numbers of invertebrates, contributing to the availability of invertebrates to be captured by the traps. However, Sayer et al. (2006) suggest that adding litter may adversely affect litter invertebrates due to reduced oxygen in the litter mass, as well as the possible addition of phytochemicals and predators. At Xishuangbanna, the different litter species resulted in significantly different invertebrate abundances which support our prediction that different species of litter will attract different herbivores and decomposers. The phenolic properties of *C. burmannii* (Penuelas et al. 2010; Li et al. 2012) are likely to have deterred herbivores and decomposers.

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Litter depth had a significant effect on invertebrate abundance. The increased invertebrate abundance was largely comprised Hymenoptera (mostly ants). The depth and structural complexity of the litter added may have been an important factor for ants. This is consistent with results from studies in Malaysia (Burghouts et al. 1992), Puerto Rico (Yang et al. 2007), and Panama (Sayer et al. 2010) which suggest that an increase in litter quantity is more important to invertebrate abundance than an increase in litter quality. The different species of litter did not influence invertebrate abundance in general, and only those plots with *L. xylocarpus* used as the litter treatments had a significantly reduced number of invertebrates. While we predicted that different species of litter would result in a different composition of invertebrates, this result is not surprising, because the four species are the dominant species of this forest, and other species would be taxonomically similar. However, it is surprising that *L. xylocarpus* caused a decline in invertebrate abundance because it is taxonomically similar to *L. hancei*, and we would have predicted that two species within the same genus would affect invertebrate decomposers in a similar manner.

Invertebrate taxa richness

At Xishuangbanna, neither litter quantity nor litter species had an effect on invertebrate richness. While we captured 16 orders of invertebrates overall, the variation of taxa richness within each pitfall trap was low with an average of only 6–8 invertebrate orders per treatment. Sayer et al. (2010) reported that at the local scale, arthropod abundance is correlated with litter mass and depth, and arthropod diversity is strongly associated with litter quality and nutrient concentrations. Therefore, it was surprising that the different species of litter used for treatments did not have an effect on invertebrate richness. Perhaps the amounts of litter used for the litter species treatments were not large enough to show effects of nutritional quality on invertebrates. We predicted that regular topping-up of litter and the resulting increased mass of litter would result in an increased invertebrate richness and abundance, but the only significant increase was for invertebrate abundance at Ailaoshan plots with the highest levels of litter addition. We can only speculate that the most extreme litter addition treatments are required to elicit a significant effect on invertebrate abundance.

Diversity and evenness

Based on previous data in invertebrate abundance and richness, it was expected that Shannon's diversity index and evenness would show similar results. In Xishuangbanna, the plots with litter removed resulted in a lower diversity and evenness than the other treatments in the litter depth experiment. This supports our prediction that as the physical and chemical properties of litter and their effects on the forest floor are removed, diversity and evenness of soil fauna is affected. In the litter species experiment, plots with *C. burmannii* had a lower diversity and evenness compared to the other treatments. The phenolic properties of *C. burmannii* are documented (Penuelas et al. 2010; Li et al. 2012) and are consistent with our conclusion that the chemical properties of leaves of this species are likely to have deterred herbivores and decomposers.

At Ailaoshan, 25 cm of litter resulted in high abundance and low richness of litter invertebrates, and this trend is reflected in the low Shannon's diversity and evenness values with the same treatment. The 25 cm plots had high numbers of ants which decreased the overall diversity and evenness values, because other orders of invertebrates were relatively much less common. In contrast, the identity of litter species had no influence on diversity or evenness in any of the treatments. The low invertebrate abundance in pitfall traps under *L. xylocarpus* was not reflected in the diversity and evenness values, so while the overall numbers were low, the relative abundance of the constituent invertebrates was quite even.

Comparative responses at the two sites

It has long been hypothesized that lower diversity ecosystems are more vulnerable to environmental fluctuations or disturbances than higher diversity ecosystems (reviewed by Hooper et al. 2005). It is argued that the higher the diversity of species the higher the amount of built-in redundancy and this redundancy acts as a buffer against change and insurance in carrying out ecological processes (Walker et al. 1999; Hooper et al. 2002). If an ecosystem is subject to stresses or disturbances, then having a higher diversity of species should reduce the likelihood of loss of ecological function. Likewise, if functions are carried out by relatively few species i.e., a lower diversity ecosystem, then this system is hypothesized to be more sensitive to change when stressed or disturbed. We detected both nutrient and invertebrate responses to litter quantity and an invertebrate response to litter species (quality) in the lower diversity forests but the only response detected in the more diverse montane forests was an invertebrate response to litter quantity. A major difference between these two forests is that the montane forest is extremely diverse while the lowland forest is less diverse. Consequently the litter composition of the montane forest is diverse but locally it could be extremely variable from patch to patch, always diverse but composed of different combinations of species. This would account for the extreme variability in soil nutrient responses in our treatments, yet at the same time explain the lack of response by the litter invertebrates—the litter is so highly diverse, abundant, and patchy that litter invertebrates are not adapted to the litter of any one tree species. In contrast, the soils litter and litter diversity of the lower diversity lowland forest will be comparatively more uniform and more susceptible to respond to changes imposed by the experimental treatments.

Conclusion

Our results show comparative patterns of soil nutrients and invertebrate abundance, composition, and richness between a tropical lowland forest (Xishuangbanna) and a tropical montane forest (Ailaoshan). Many of the differences may be attributed to the general temperature and rainfall conditions at the sites. At the local scale, differences in soil nutrients and invertebrate abundance may partially be explained by litter. We conclude that more diverse forests are less susceptible to change than lower diversity forests and that litter abundance has a much more significant impact on soil nutrients and litter invertebrates than litter species composition.

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