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Plant litter quality influences the contribution of soil fauna to litter decomposition in humid tropical forests, southwestern China

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ABSTRACT

The aim of this field experiment was to quantify the contribution of soil fauna to plant litter decomposition in three forest sites differing in C/N ratio under natural conditions in Xishuangbanna, southwestern China. We conducted a survey of soil fauna communities, the forest floor litter and investigated mass loss of mixed tree species leaf litter for two years in a tropical secondary forest, an evergreen broad-leaf forest and a tropical rain forest. Exclusion treatments of different sized soil fauna from the leaf litter by using varying mesh size litter bags (2 mm and 0.15 mm) were also performed. Mass loss and C and N concentrations in litter bag leaf materials were determined at monthly intervals. We found that: (1) the three forests differed in floor litter biomass and nutrient contents but not in soil fauna richness and abundance; (2) litter mass loss and decomposition rate were slower when soil macrofauna and most of mesofauna were excluded; and (3) greatest soil fauna contribution to plant litter decomposition occurred in the rain forest, where leaf litter C/N ratio was also highest (41.5% contribution: 54.8 C/N ratio), in comparison to 8.69% in the broad-leaf forest and 19.52% in the secondary forest, both with low leaf litter C/N ratios (<32). Our results suggested that, soil fauna played a more pronounced role in the decomposition of mixed leaf litter in tropical rain forest, and significantly bigger effects from fauna were ascribed to the enhancement of N concentration and decrease of C concentration of the initially high C/N ratio litter in this forest site.

1. Introduction

Decomposition process of plant residues is influenced by substrate quality, decomposer community and environmental factors (Swift et al., 1979; Coleman and Crossley, 1996; Smith and Bradford, 2003). Within a given climatic region, litter chemistry is the main determinant of litter decomposition (Vitousek and Sanford, 1986). Litter decay and nutrient release are controlled by the litter quality, including the nitrogen (N) concentration of the litter, the carbon to nitrogen (C/N) ratio, as well as other chemical properties (Aerts, 1997; Aerts and De Caluwe, 1997; Vitousek et al., 1994; Shaw and Harte, 2001; Blair et al., 1990). Faster decomposition rates are often associated with lower C/N ratios (Swift et al., 1979) and high initial N concentration (Bosatta and Staaf, 1982).

Soil fauna are an important component in forest ecosystems, due to their functional role in the acceleration of organic matter decomposition and nutrient transformations (Seastedt and Crossley, 1980, 1983; Bardgett and Chan, 1999; Hasegawa and Takeda, 1996). The positive influence of soil fauna on plant litter decomposition is widely known and well accepted for many ecosystems (McBrayer and Reichle, 1971; Seastedt, 1984). Soil fauna largely control the decomposition process through breakdown of litter, digestion, and stimulation of micro-organism activities (Petersen and Luxton, 1982; Anderson et al., 1983; Byzov et al., 1996; Maraun and Scheu, 1996). Soil fauna represent multiple trophic roles. For example, earthworms, enchytraeid worms and millipedes are detritivores while collembola and mesostigmata act as fungivores and predators, respectively (Lavelle et al., 1993; Lavelle and Spain, 2001). This function diversity influences decomposition in a variety of direct and indirect ways (Lavelle et al., 1993; Lavelle and Spain, 2001; Seastedt and Crossley, 1980; González and Seastedt, 2000). A common way to manipulate functional diversity in soil fauna is to exclude different size-groups of soil fauna with varying sizes of mesh (Irmler, 2000; Hunter et al., 2003; Barajas-Guzmán and Alvarez-Sánchez, 2003).

The fauna effect on decomposition often can vary with forest type. For example, Heneghan et al. (1998, 1999a,b) demonstrated mass loss contributed by the fauna was much faster in tropical

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forests than in temperate forest. González and Seastedt (2000, 2001) also suggested that the fauna effect on decomposition in tropical wet forest was significantly higher than tropical dry forest. These differences were often ascribed by the different fauna richness and abundance in different forest types. However, experiments across climatic conditions with varying resource quality, i.e., often on the basis of some single litter species decomposition, indicated that the soil fauna effect on decomposition differed significantly under different climates and resource quality as measured by C/N ratios (González and Seastedt, 2000, 2001; Heneghan et al., 1998, 1999a,b).

Forest dynamics by natural succession and human land use changes can influence composition of the soil fauna community due to changes in plant species composition and vegetation structure (Koehler and Born, 1989) that result in changes in plant litter quality and quantity (Wardle et al., 2006; Cadisch and Giller, 1997; Badejo and Tian, 1999) and micro-environmental conditions (Vitousek and Walker, 1989). Mixtures of different litter types may be structurally more complex than homogeneous litter and have more decomposition stages, thus reducing competition between decomposers and offering an opportunity for the coexistence of many animal species and individuals (Hansen and Coleman, 1998). Litter mixtures influence microbial and faunal activity and thus the way that the litter is decomposed, even at a local scale or more small area (Sulkava and Huhta, 1998; Sulkava et al., 1996; Blair et al., 1990; Irmler, 2000). However, how the litter quality in different forests influences the contribution of soil fauna on litter decomposition is still not fully explored.

Xishuangbanna, Yunnan Province, China, is an ecotone between the Asian tropical and subtropical forests and is an important area for conservation due to its extensively rich biodiversity (Zhu, 1992; Zhang and Cao, 1995; Cao et al., 2006; Zheng et al., 2006). Within Xishuangbanna, different types of forests often occur in the same area due to elevation changes, intensive human land use and the dynamics of forest development history. Thus, it is an ideal place to understand how soil fauna composition differs across forests sites and how their effect upon decomposition varies under similar climatic conditions.

We designed our study to answer the following questions in tropical forests of Xishuangbanna: (1) How do litter quality (C/N ratio), soil property and fauna communities vary among different sites? (2) What is the contribution of soil fauna to the decomposition of plant litter, and how does their contribution correspond to plant litter quality across these tropical forest sties in Xishuangbanna?

2. Materials and methods

2.1. Study sites

Our study was conducted in the main research sites of the Chinese Ecological Research Network (CERN) in Xishuangbanna tropical area (101°46′E, 21°54′N), SW China. We selected three different tropical forest sites located in close proximity to each other in the Menglun Nature Reserve (650–750 m in elevation, 101°11′E, 21°56′N). This region has a tropical monsoon climate. Mean annual air temperature is 21.5 °C, ranging from 14.8 °C in the coldest month (January) to 25.5 °C in the hottest month (June), with zero days of frost. Annual precipitation is about 1500–1600 mm, of which 85–90% occurs in rainy season between May–October, and 10–15% occurs in dry season between November–April. The soil type in the study sites is red Ultisol.

Our three sites varied in annual litter fall and plant species composition. The tropical rain forest site is a tropical seasonal rain forest over 100 years old (Zhang and Cao, 1995). The canopy is uneven and consists principally of megaphanerophytes over 40 m tall. The most abundant species are *Pometia tomentosa* Teysm. Et Binn, *Amoora tetrapetala* C.Y. Wu, *Gironniera subaequalis* Planch, *Terminalia myriocarpa* Heurck et Muell.-Arg, *Chisocheton siamensis* Craib *Myristica fragrans* Houtt, *Mitrephora wangii* Hu, *Barringtonia macrostachya* Kurz, *Knema furfuraceea* Warb and *Baccaurea ramiflora* Lour et al. (Zhu, 2006). Annual litter fall is $83.8 \pm 4.0\ g\ m^{-2}$ (mean ± SE, CERN unpublished data).

The broad-leaf forest site is a 70–80 year old evergreen broad-leaved forest with a low canopy (20–25 m) composed mainly of *Lithocarpus truncates* Rehd. et Wils., *Castanopsis mekongensis* A. Camus, *Wendlandia bouvardioides* Hutch., *C. mekongensis* A. Camus, *Castanopsis echinocarpa* A. DC., *Castanopsis carlesii* Chun var. *spinuposa* Cheng et C.S. Chao et al. (Zhang and Cao, 1995). The annual litter fall is $107.6 \pm 7.3\ g\ m^{-2}$ (mean ± SE, CERN unpublished data).

The secondary forest site is a tropical secondary forest and is dominated by 30–40 year old successional tree species that recolonized the area after it was no longer used for agriculture. The canopy is low (20–25 m) and composed mainly of speciesof *Litsea monopetala* Pers., *Millettia laptobotrya* Dunn, *Castanopsis indica* A. DC., *Schefflera octophylla* Harms, *Macaranga denticulata* Muell.-Arg., *Mallotus paniculatus* Muell.-Arg., *Bauhinia variegata* Linn. var. *candida* Voigt., *Phyllanthus emblica* Linn et al. (Zhang and Cao, 1995). The annual litter fall is $122.3 \pm 7.9\ g\ m^{-2}$ (mean ± SE, CERN unpublished data).

The initial C and N concentrations of mixed leaf litter in the secondary and broad-leaf forest sites are significantly different from the rain forest and subsequently the secondary forest and broad-leaf forest have lower C/N ratios than the rain forest (Table 1). More detailed descriptions of the geomorphology, vegetation, soil and land use history in these three sites can be found in Zhu (2006) and Zhang and Cao (1995).

2.2. Floor litter, soil and soil fauna surveys

In order to compare the micro-environment of forest floor litter and soil, we collected ten samples of forest floor litter and mineral soil in each of the three forest locations during September 2000 (rainy season) and May 2001 (end of dry season). We established a 50 m transect in each location and collected forest floor litter of 30 × 30 cm and soil cores of 5 cm diameter and 10 cm deep within 30 × 30 cm plots located 5 m apart along the transect, for a total of ten samples. Litter and soil samples were stored in plastic bags and transferred to the laboratory for immediate processing.

Soil fauna were extracted from the floor litter using Tullgren ("Berlese") funnels for four days (Crossley and Coleman, 1999) and collected in 90% ethanol. Soil fauna were identified to order and counted using a microscope.

After soil fauna were extracted, the forest floor litter was oven dried at 60 °C until a constant weight was obtained. Following drying, litter samples were divided into three fractions, leaf, wood, and miscellaneous components (such as seeds, flower and humus, Brady, 1990) by hand sorting. Each litter fraction was weighed and total sample dry mass was calculated as the sum of the fractions.

Table 1
Initial percentage composition of C (%), N (%) and C/N ratios of three leaf litter types in litter bags at start of experiment (mean ± 1SE).

Sites	C	N	C/N
Secondary forest	47.87 (2.3)a	1.32 (1.06)a	28.9 (2.3)a
Broad-leaf forest	48.55 (3.95)a	1.55 (0.7)a	31.8 (1.6)a
Rain forest	49.87 (2.5)b	0.9 2 (0.22)b	54.8 (1.3)b

Different letters represent significant difference within column ($p < 0.05$).

Five soil (every two neighboring samples of total 10 combined to one) and ten litter samples were ground in a Wiley mill (mesh size #20) for chemical analyses. Floor litter samples were analyzed for total C and total N, while mineral soil samples analyzed for pH, organic matter, total N, total P and Ca in the biogeochemistry laboratory in Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences.

For chemical analyses, total N was determined using a micro-Kjeldahl method, digesting 0.5 g subsamples in H_2SO_4 and H_2O_2 solution. Total C and soil organic matter were determined by digesting subsamples in $K_2Cr_2O_7$–H_2SO_4 (National Forest Service of China, 1999). Total P and Ca of soil were determined by digestion with HNO_3 and $HClO_4$ and were analyzed using an ICP-AES (Thermo Jarrell Ash Corporation, USA). Soil pH (1:1 paste of soil and de-ionized water) were analyzed on fresh soils.

2.3. Leaf litter bag decomposition experiments design

Litter bag decomposition experiments were set up at three forest sites from 2001 until 2002. We selected 2 mm and 0.15 mm nylon mesh bags (15 × 20 cm) according to the body size (width) of litter fauna (Swift et al., 1979). It is expected that most macro, meso, and microfauna can move into the 2 mm bags, thus we treat these as our control bags. Only microfauna, such as Protozoa and Nematoda may invade the 0.15 mm mesh bags, thus excluding most macro and mesofauna.

During the peak litter fall period between March and April of 2001, mixed species leaf litter was collected on nylon nets in each forest site. The litter was air-dried in the laboratory and 30 g of dry mixed leaf litter was placed in each bag. In each of the three forest sites, we established one 50 × 50 m plot. Within each plot, we erected an evenly spaced 10 row × 12 column sampling grid and placed one litter bag of each mesh size at each sampling point along the grid on the forest floor just above the mineral soil. Thus each forest type had 120 2 mm mesh size bags, and 120 0.15 mm mesh size bags. Bags were placed in the forest in April 2001 and the last sampling date was May 2002. A subsample of 30 bags (10 litter bags per sites) was collected and returned to the laboratory immediately after placement in the field. These bags were oven dried at 60 °C until they reached a consistent weight in order to establish handing loss, initial dry mass and C, N concentration (Seastedt et al., 1992).

Each month over the course of a year, a row of ten bags per mesh size was retrieved from each forest, sealed in a plastic bag and returned to the laboratory. Macrofauna were collected by hand from the litter bags first, then the materials were exposed to heat extraction in a Tullgren funnel as described above. Fauna were identified after sorting to order.

Following each faunal extraction, treated litter was quickly cleaned in pure water to remove mineral soil from the litter. Litter materials including any fragments were dried in an oven (60 °C) and reweighed to determine the remaining mass. Dry, ground leaf samples were analyzed for C and N as described above.

2.4. Statistical analyses

The fauna data from the survey and experiment are presented as order richness (number of orders and relative density of orders), abundance (density and relative density). Fauna density refers to the number of individuals per square meter, whereas fauna relative density of orders and individuals refers to the number of orders and individuals per gram of dry litter. In addition, we calculated several fauna diversity metrics: Shannon–Wiener Index ($H(o)$; Shannon and Weaver, 1949), evenness as $H(o)$ divided by the maximum of $H(o)$ (E; Pielou, 1966) and Margalef index (D; Magurran, 1988).

For the experiment, leaf mass loss rate (k) in the litter bags with different mesh sizes was estimated using Olson's formula (Olson, 1963): $X_t = X_0 \cdot e^{-kt}$, where X_t is mass remaining at time t, X_0 was mass at $t = 0$, and k is annual mass loss rate.

Following Seastedt (1984) the mass loss as contributed by the soil fauna (fauna effect) was calculated by using the formula: fauna effect = (Control litter bags − Treated litter bags)/Control litter bags; where control litter bags are mass loss of 2 mm mesh size litter bags, and treated litter bags are mass loss of 0.15 mm mesh size bags.

Two-way ANOVA analyses were performed to test for treatment effects of time and mesh size (fixed factors) on the mass loss of the leaf litter in litter bags. One-way ANOVA was used to test for decomposition rate, differences in the mean number of orders, and individual density of the various litter fauna groups in floor litter and litter bags among forests. Paired t-test analyses were used to test for differences in mass loss, decomposition rate, C, N concentration and litter fauna diversity between mesh sizes. To test the relationship between soil fauna richness (Order g^{-1} dry litter) (González and Seastedt, 2000) and annual decomposition rate within site (ten points, each point is the average of twelve collections at each site), we used linear correlation analysis based on the data of the 2 mm mesh bags. Also, we examined the correlations between the fauna effect and initial C, N remaining at each time sample point during the decomposition experiment (where fauna effect and initial C, N remaining are the average per collecting date over twelve collections). Data were tested for homogeneity of variance using Levene's test of equality of error variances and skewness (SPSS 9.0 Win). Log-transformations were employed when the data did not meet the assumptions of normality. The level of significance was set at $\alpha = 0.05$.

3. Results

3.1. Forest floor litter and soil chemistry

Our forest floor litter survey revealed differences in biomass (LSD: $F = 13.797$, $p < 0.0001$) and leaf chemistry (C: $F = 7.165$, $p = 0.005$; C/N: $F = 9.077$, $p = 0.002$) among the three study sites. Broad-leaf forest had the highest amount of floor litter biomass, while the rain forest had the highest C concentration and C/N ratio of floor litter. Sites did not differ in N concentration of floor litter ($F = 1.011$, $p = 0.382$). The only soil chemistry parameter that differed significantly among sites was C/N ratio ($F = 4.02$, $p = 0.05$). The rain forest had a lower C/N ratio of soil than the secondary forest ($p = 0.021$) and the broad-leaf forest ($p = 0.049$) (Table 2).

3.2. Soil fauna

3.2.1. Floor litter across the three sites

A total of 24 different soil fauna groups (orders) were recorded in floor litter (Table 3) during the dry and rainy season surveys. Acari dominated the density of litter fauna, and composed 42.9–75.4% of total individuals across different forests and seasons. Collembola, Hymenoptera (ants) and Coleoptera were the second, third and fourth most abundant litter fauna component respectively in all three forest sites (Table 3).

Different forest sites did not differ in fauna density and richness, while the Shannon–Wiener index ($F = 22.534$, $p < 0.001$) and the evenness index ($F = 23.523$, $p < 0.001$) of fauna were significantly different among forest sites in the dry season. The secondary forest had a significantly higher Shannon–Wiener index and evenness index compared to tropical rain forest and broad-leaf forest in the dry season (Table 3).

Table 2
Comparison of floor litter and soil chemistry in three forest sites (mean ± 1SE, floor litter $n = 10$; soil chemistry $n = 5$).

Forest type	Floor litter (total floor)				Soil chemistry (0–10 cm)					
	Biomass ($g\,m^{-2}$)	C %	N %	C/N	pH	O.M. %	T.N %	T.P %	T.Ca %	C/N
Secondary forest	468.1 ± 67.8a	37.4 ± 1.5a	1.6 ± 0.1a	23.5 ± 0.8a	4.3 ± 0.1a	4.3 ± 0.4a	0.2 ± 0.01a	0.04 ± 0.001a	0.03 ± 0.002a	21.9 ± 0.8a
Broad-leaf forest	836.6 ± 63.7b	40.8 ± 1.1ab	1.6 ± 0.1a	26.4 ± 1.2a	4.5 ± 0.1a	3.9 ± 0.3a	0.2 ± 0.02a	0.03 ± 0.002b	0.03 ± 0.003a	21.2 ± 0.9a
Rain forest	406.1 ± 67.8a	44.3 ± 1.1b	1.5 ± 0.1a	30.8 ± 1.2b	4.5 ± 0.1a	3.7 ± 0.3a	0.2 ± 0.01a	0.04 ± 0.002a	0.04 ± 0.002a	18.4 ± 1.0b

Different letters represent significant difference within column ($p < 0.05$).

Among the twenty-four fauna groups, the amounts of Enchytraeidae, Protura, Diptera larvae, Acari, Thysanoptera, Lepidoptera, Orthoptera, Pseudoscorpiones and Aranene differed among three forest sites in the dry season. Enchytraeidae and Hymenoptera (ants) differed during the rainy season (Table 3).

3.2.2. Faunal exclusion treatments

Applications of 2 mm mesh size litter bags did not decrease taxonomic diversity or density of total soil fauna as compared to natural floor litter (survey data) in the same forest site (Table 4). The 0.15 mm mesh size litter bags were effective in reducing the abundance of most macro, meso and microfauna during decomposition compared to the 2 mm mesh bags in all three sites. Only a few fauna groups were found in 0.15 mm mesh size litter bags (Table 4). Compared to the 2 mm mesh bags, using 0.15 mm litter bags resulted in a reduction in the individual abundance of total fauna (individuals g^{-1} dry litter) of 69.9% in secondary forest, 73% in broad-leaf forest and 81.4% in rain forest, and a reduction of fauna orders richness (Orders g^{-1} dry litter) of 76.8% in secondary forest, 69.8% in broad-leaf forest and 88.4% in rain forest (Table 4).

3.3. Leaf litter decomposition and dynamic of C, N

Annual litter mass losses were larger in the 2 mm mesh than that in the 0.15 mm mesh bags in all three sites. There were significant mesh size treatment effects on mass loss in all three sites (secondary forest: $F = 105.944$, $p < 0.001$; broad-leaf forest: $F = 23.88$, $p < 0.001$; rain forest: $F = 666.81$, $p < 0.001$). A treatment × time interaction was observed in the broad-leaf forest ($F = 2.39$, $p = 0.008$) and rain forest ($F = 9.25$, $p < 0.001$), but not in the secondary forest ($F = 0.477$, $p = 0.916$) (Fig. 1).

Mean annual decay rates (k) of mixed leaf litter in the 2 mm mesh bags were higher than that in the 0.15 mm mesh bags in all three forests, and there was a significant treatment effect on decay rates (k) of different mesh size bags in the rain forest ($T = 7.591$, $p < 0.001$) and broad-leaf forest ($T = 2.587$, $p = 0.029$), but not the secondary forest ($T = 1.799$, $p = 0.106$) (Table 5).

The calculated contributions of soil fauna to the mass loss of mixed litter were higher in rain forest than those in the broad-leaf forest and secondary forest (Table 5). The positive correlations between order richness (Orders g^{-1} dry litter) and decay rate ($K_{2\ mm}$) values in the 2 mm litter bags in the broad-leaf forest ($r = 0.715$, $p = 0.02$) and rain forest sites ($r = 0.708$, $p = 0.02$) were found, but not in the secondary forest site.

There was a significant effect of mesh size on the final C (secondary forest: $T = 4.743$, $p = 0.001$; broad-leaf forest: $T = 5.069$, $p = 0.001$; rain forest: $T = 2.703$, $p = 0.035$) and N (secondary forest: $T = 6.283$, $p < 0.001$; broad-leaf forest: $T = 7.233$, $p < 0.001$; rain forest: $T = 3.553$, $p < 0.012$) concentration of different forest mixed litter. On average, the final C and N concentrations of all sites mixed litter were lower in the 2 mm mesh bags than those in the 0.15 mm mesh bags. N concentration increased significantly over the duration of the experiment in all three forest sites in the 0.15 mm mesh bags, while only rain forest showed significant increases in N concentration in the 2 mm mesh bags (from initial 0.919 ± 0.22 to final 1.321 ± 0.05; mean ± SE; $T = 8.918$, $p < 0.001$) for the duration of the experiment.

The C/N ratios of mixed litter were not significantly different between 2 mm and 0.15 mm mesh size bags in all three sites during the experiment (data not shown), but there was a larger decrease of mixed litter C/N ratio in 2 mm mesh bag from initial (54.8 ± 1 .9, mean ± SE) to final (22.4 ± 2.4) in the rain forest site in comparison to broad-leaf forest (from 31.8 ± 1.8 to 20.3 ± 0.6) and secondary forest (from 28.9 ± 0.6 to 19.6 ± 0.8) sites.

The percentages of initial C (secondary forest: $t = 19.545$, $p < 0.001$; broad-leaf forest: $t = 12.379$, $p < 0.001$; rain forest: $t = 21.032$, $p < 0.001$) and N (secondary forest: $t = 20.517$, $p < 0.001$; broad-leaf forest: $t = 13.854$, $p < 0.001$; rain forest: $t = 37.146$, $p < 0.001$) remaining in 2 mm mesh bags were significantly lower than those in 0.15 mm mesh bags in both three forest sites and the percentages decreased gradually through the course of the experiment in secondary forest and broad-leaf forest sites (Fig. 2). In the rain forest, strong initial N immobilization resulted in a rise in the percentage of initial N remaining in 2 mm mesh bags in the first month, and in 0.15 mm mesh bag during the first three months of the experiment. After the first 30 days, however the percentage of initial N remaining in the 2 mm mesh bags decreased strongly while it also started to decrease in the 0.15 mm mesh bags after 90 days and N remained immobilized in the litter above 100% of initial amounts until the end of experiment (Fig. 2). The initial C and N remaining in mixed litter was negatively correlated to the mass loss contributed by soil fauna (fauna effect) in rain forest (C: $r = 0.834$, $p = 0.001$; N: $r = 0.821$, $p = 0.001$), whereas no correlation between initial C and N remaining in mixed litter and the fauna effect were found in secondary forest (C: $r = 0.373$, $p = 0.232$; N: $r = 0.419$, $p = 0.175$) and broad-leaf forest (C: $r = 0.302$, $p = 0.242$; N: $r = 0.195$, $p = 0.258$).

4. Discussion

4.1. Soil fauna community

The overall similarity of soil fauna composition in both leaf litter and exclusion treatments among three different forest sites indicates the important role of climatic and biogeographic conditions in the assembly of these communities (Coleman and Crossley, 1996; Hartmut, 1998; Yin et al., 2000). At the landscape scale, the vegetation composition, plant species diversity, mixing of plant litter types, and aboveground tropic interaction, all impact on soil fauna diversity (Wardle et al., 2006). In our study, small differences among sites existed, and a significantly higher amount of some groups (description in result Section 3.2) and diversity index occurred in secondary forest during the dry season. These differences in the abundance of groups may reflect differences in litter input caused by a litter fall peak (from March to April), which may influence the efficiency of colonization across different forest sites under the same climatic conditions (Sulkava et al., 1996; Hansen and Coleman, 1998; Sulkava and Huhta, 1998; Wardle et al., 2006).

Table 3
Comparison of soil fauna community and diversity in the floor litter across the three study sites during dry and rainy season (mean ± 1SE, $n = 10$).

Functional groups and taxonomic order	Dry season						Rainy season					
	Secondary forest		Broad-leaf forest		Rain forest		Secondary forest		Broad-leaf forest		Rain forest	
	Density	%	Density	%	Density	%	Density	%	Density	%	Density	%
Detritivorous												
Isopoda	4.6 ± 2.5ab	0.1	11.9 ± 6.9a	0.2	0.9 ± 0.9b	0.02	16.5 ± 4.7a	0.2	4.6 ± 2.5a	0.1	11.9 ± 5.1a	0.2
Diplopoda	79.9 ± 17.9a	2.4	14.7 ± 7.1a	0.2	25.7 ± 9.8a	0.6	106.5 ± 40.6a	1.5	102.8 ± 45a	1.5	100.1 ± 36.6a	1.8
Symphyia	5.5 ± 1.5a	0.2	21.1 ± 6.1b	0.3	5.5 ± 2.3a	0.1	14.7 ± 11a	0.2	10.1 ± 8.2a	0.1	9.2 ± 36.6a	0.2
Demaptera	0.9 ± 0.9a	0.0	6.4 ± 2.4b	0.1	2.8 ± 1.9ab	0.1	0a	0.0	1.8 ± 1.2a	0.0	1.8 ± 1.2a	0.0
Isoptera	3.7 ± 1.5a	0.1	1.8 ± 1.8a	0.0	0.9 ± 0.9a	0.02	6.4 ± 3.9a	0.1	0a	0.0	0a	0.0
Enchytraeidae	12.9 ± 4.7a	0.4	11.9 ± 6.5a	0.2	67.0 ± 20b	1.6	2.3 ± 1.3a	0.0	7.4 ± 3.4a	0.1	33.06 ± 9.8b	0.6
Saprophagous												
Blattodea	2.8 ± 1.4a	0.1	5.5 ± 2.4a	0.1	1.8 ± 1.2a	0.0	3.7 ± 2a	0.1	2.8 ± 1.4a	0.0	4.6 ± 2.1a	0.1
Diptera larvae	325.1 ± 39.2a	9.6	76.2 ± 9.8b	1.2	94.6 ± 33.5b	2.3	76.2 ± 21.1a	1.1	58.8 ± 12.3a	0.8	154.3 ± 64.6a	2.7
Coleoptera	143.3 ± 12.9a	4.2	178.2 ± 31.6a	2.8	232.3 ± 56.7a	5.6	173.6 ± 53.1a	2.4	222.2 ± 77.9a	3.1	202.0 ± 43a	3.5
Omnivorous												
Acari	1452.7 ± 1.4a	42.9	4753.9 ± 1102.6b	73.9	2716.3 ± 760.3ab	65.6	4932.1 ± 1538.4a	68.9	5324.2 ± 1057.4a	75.4	3517.0 ± 884.1a	61.7
Hymenoptera (Ants)	343.4 ± 144.9a	10.2	223.1 ± 56.8a	3.5	141.4 ± 38.4a	3.4	254.4 ± 40.3a	3.6	318.6 ± 59.3a	4.5	80.8 ± 22.9b	1.4
Fungivorous												
Collembola	554.6 ± 139.5a	16.4	616.2 ± 208.5a	9.6	707.1 ± 290a	17.1	1348.0 ± 379.4a	18.8	870.5 ± 212.7a	12.3	1385.7 ± 339.9a	24.3
Protura	55.1 ± 19a	1.6	14.7 ± 4.9b	0.2	17.4 ± 8.4b	0.4	3.7 ± 2.8a	0.1	5.5 ± 3.7a	0.1	15.6 ± 6.6a	0.3
Thysanoptera	168.9 ± 28.4a	5.0	241.5 ± 88.4a	3.8	0b	0.0	8.3 ± 2.9a	0.1	7.3 ± 3.8a	0.1	9.2 ± 7.2a	0.2
Psocoptera	52.3 ± 12.2ab	1.5	68.9 ± 17.9a	1.1	30.3 ± 8b	0.7	11.9 ± 5.3a	0.2	4.6 ± 1.5a	0.1	7.4 ± 2.3a	0.1
Pauropoda	11.0 ± 7.3a	0.3a	8.3 ± 3.7a	0.1	3.7 ± 1.9a	0.1	2.8 ± 2a	0.0	12.6 ± 3.1a	0.2	11.02 ± 5.6a	0.2
Phytophagous												
Orthoptera	6.4 ± 2.4a	0.2	0b	0.0	0.9 ± 0.9b	0.0	0a	0.0	0.9 ± 0.9a	0.0	1.8 ± 1.2a	0.0
Hemiptera	15.6 ± 2.4a	0.5	19.3 ± 9a	0.3	23 ± 9.1a	0.6	76.2 ± 17.6a	1.1	47.8 ± 18.8a	0.7	68.0 ± 14.7a	1.2
Homoptera	12.9 ± 2.4a	0.4	35.8 ± 10.3b	0.6	12.9 ± 3.9a	0.3	12.9 ± 7a	0.2	13.8 ± 5.2a	0.2	5.5 ± 2.5a	0.1
Lepidoptera	50.5 ± 11.6a	1.5	42.2 ± 8.6a	0.7	13.8 ± 3.5b	0.3	4.6 ± 2.8a	0.1	3.7 ± 2a	0.1	4.6 ± 2.5a	0.1
Carnivorous												
Diplura	1.8 ± 1.2a	0.1	0b	0.0	1.8 ± 1.7a	0.04	0a	0.0	0.9 ± 0.9a	0.0	1.8 ± 1.2a	0.0
Aranene	57.9 ± 12.9a	1.7	37.6 ± 7.3ab	0.6	23 ± 6.8b	0.6	27.5 ± 8.2a	0.4	12.9 ± 3.7a	0.2	41.3 ± 15.9a	0.7
Pseudoscorpiones	20.2 ± 6.1ab	0.6	25.7 ± 7.1a	0.4	5.5 ± 2.7b	0.1	18.4 ± 7.7a	0.3	13.8 ± 7.2a	0.2	19.3 ± 7.8a	0.3
Chilopoda	0.9 ± 0.9a	0.0	11.9 ± 5.7b	0.2	5.5 ± 3ab	0.1	6.4 ± 2.4a	0.1	13.8 ± 3.4a	0.2	11.02 ± 4.7a	0.2
Total (ind. m^{-2})	3382.9 ± 517.8a	100.0	6429.8 ± 1326.6a	100.0	4139.6 ± 1121.3a	100.0	7161.6 ± 1991.5a	100.0	7063.4 ± 1314.9a	100.0	5697.0 ± 1256.1a	100.0
Fauna Diversity												
Number of Order	15.7 ± 0.7a		16.7 ± 1.0a		13.3 ± 1.4a		13.5 ± 1.3a		13 ± 0.5a		13.6 ± 1.3a	
Shannon index (H′)	1.9 ± 0.1a		1.1 ± 0.07b		1.2 ± 0.1b		1.2 ± 0.2 ab		0.9 ± 0.3a		1.2 ± 0.1b	
Evenness index (E)	0.4 ± 0.01a		0.3 ± 0.02b		0.3 ± 0.03b		0.3 ± 0.02a		0.2 ± 0.03a		0.3 ± 0.02a	
Margalef index (D)	1.8 ± 0.1a		1.8 ± 0.1a		1.5 ± 0.2a		1.4 ± 0.1a		1.4 ± 0.05a		1.5 ± 0.1a	
Relative density of Ind.	6.6 ± 517.8a		8.5 ± 1.5a		6 ± 1.5a		13.9 ± 3.4a		16.8 ± 2.7a		18.6 ± 5.9a	
Relative density of order	0.4 ± 0.02a		0.2 ± 0.01a		0.2 ± 0.03a		0.4 ± 0.03a		0.3 ± 0.02a		0.4 ± 0.1a	

Different letters represent significant difference between forest sites within same season ($p < 0.05$).

Table 4
Comparison of soil fauna between two mesh size bags after a 12 month decomposition period at three forest sites (mean (SE), $n = 10$).

Treatment	Forest sites	Acari	Collembola	Ants	Diplopoda	Enchytraeidae	Aranene	Individual abundance	Order richness	Shannon–Wiener
		(Ind. g^{-1} dry litter)	(Ind. g^{-1} dry litter)	(Ind. g^{-1} dry litter)	(Ind. g^{-1} dry litter)	(Ind. g^{-1} dry litter)	(Ind. g^{-1} dry litter)	(Ind. g^{-1} dry litter)	(Order. g^{-1} dry litter)	Index (H′)
2 mm mesh size	Secondary forest	7.02 (1.56)aA	3.72 (0.65)aA	1.05 (0.35)aA	0.22 (0.12)aA	0.07 (0.02)aA	0.58 (0.16)aA	14.9 (2.65)aA	1.21 (0.15)aA	1.33 (0.02)aA
	Broad-leaf forest	3.3 (0.8)aB	1.75 (0.39)aB	1.24 (0.33)aA	0.12 (0.06)aA	0.03 (0.01)aA	0.28 (0.08)aB	7.56 (1.74)aB	0.86 (0.06)aB	1.30 (0.02)aA
	Rain forest	4.15 (1.11)aB	3.76 (0.77)aA	1.08 (0.36)aA	0.16 (0.05)aA	0.39 (0.24)aB	0.41 (0.12)aA	10.52 (2.07)aB	1.55 (0.32)aA	1.38 (0.03)aA
0.15 mm mesh size	Secondary forest	2.55 (0.6)aA	1.33 (0.2)bA	0.03 (0.03)bA	0.005 (0.004)bA	0.05 (0.02)aA	0.01 (0.003)bA	4.49 (0.84)bA	0.28 (0.04)bA	0.74 (0.02)bA
	Broad-leaf forest	1.3 (0.08)bB	0.82 (0.12)bB	0.06 (0.06)bA	0.008 (0.01)bA	0.03 (0.01)aB	0.1 (0.07)aB	2.04 (0.31)bB	0.26 (0.03)bA	0.84 (0.02)bB
	Rain forest	0.96 (0.28)bB	0.96 (0.16)bB	0.05 (0.03)bA	0.004 (0.001)bA	0.05 (0.02)bA	0.01 (0.002)bA	1.96 (0.58)bB	0.18 (0.02)bB	0.69 (0.02)bA

Different capital letters in a column indicate significant difference between sites with the same mesh size bags. Different small letters within the same column indicate a significant difference between mesh size treatments at the same sites ($p < 0.05$).

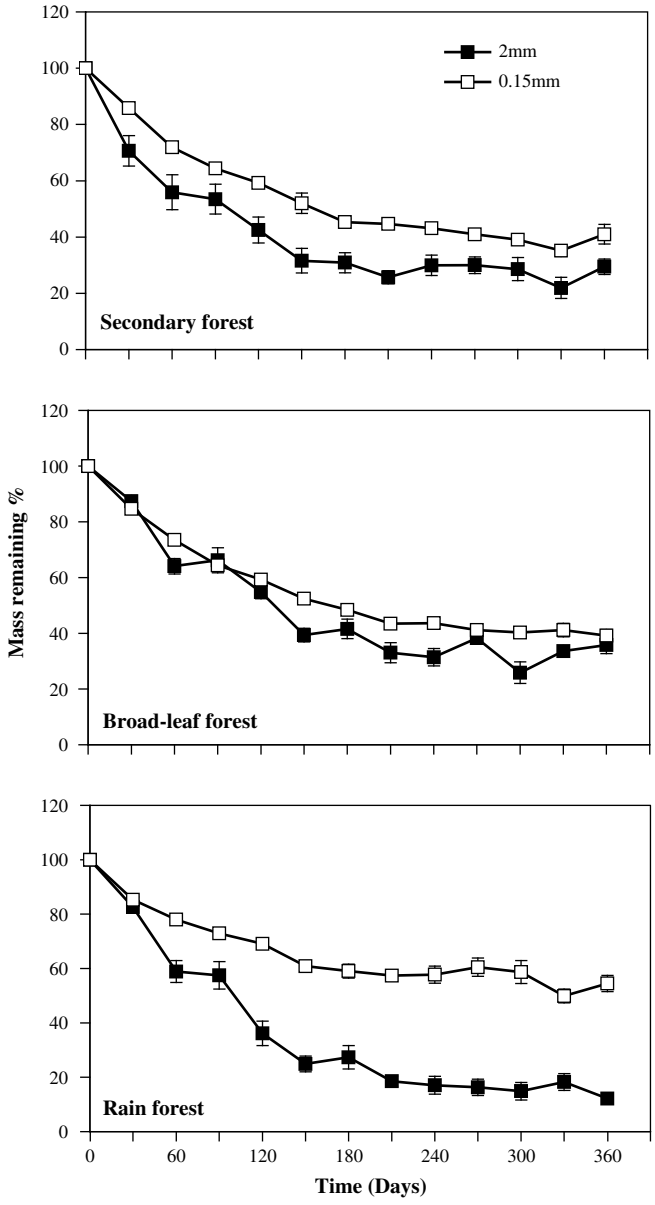

Fig. 1. Changes in the mass remaining of litter in 2.0 mm and 0.15 mm mesh size litter bags overtime in three forest sites. (Mean ± SE, $n = 10$.)

The variation of abundance for certain soil fauna groups and fauna diversity often responds to litter quantity and quality change during succession and forest type (Wardle et al., 2004, 2006; Milcu et al., 2006), For example, Barajas-Guzmán and Alvarez-Sánchez (2003) and Oliver (1981) found that fauna richness did not differ between secondary forest and rain forest, but diversity index was higher in the secondary forest, which seems to agree with our results for soil faunal diversity.

4.2. Soil fauna effect and in relation to litter C/N ratio

The N concentrations of mixed leaf litter in the rain forest were significantly lower than that in the secondary and broad-leaf forests while the C/N ratio was significantly higher than the two forests. Similar results were obtained by Jeffrey and Timothy (1994), who reported that the leaves of old-growth forest species had a significantly lower initial N concentration and higher C/N ratio than did the leaves of succession species. The nutrient availability declines from early to late succession, plants shift allocation from growth to plant defense to herbivores (Chapin et al., 2002; Milcu et al., 2008; Xiang and Chen, 2004). Plant species composition in forest may also affect mixed litter quality (Brown and Lugo, 1990), for example, in this study, the dominant species in broad-leaf forest were plant species in Fagaceae family which often have relative high N concentration and low C/N ratio (Liu et al., 2002).

According to Lavelle et al's. (1993) model, it can be expected that under constant climate and a similar community of soil organisms, litter quality would be the most important factor regulating decomposition. Therefore we expected that the high litter quality (low C/N) in secondary forest and broad-leaf forest would lead to accelerated decomposition. Our data from the 0.15 mm mesh bags that excluded most soil fauna supported this hypothesis. However, the data from the 2 mm mesh bags (fauna accessible bags) did not accord with this pattern. The decomposition rate (k value) of mixed litter in the 2 mm mesh bags in rain forest was significantly higher than those in the other two forests (Table 5).

The present study demonstrated that the soil fauna community played a more substantial role in leaf litter decomposition in the tropical rain forest than the broad-leaf forest and the secondary forest by significantly accelerating decomposition rate. A marginal but significant effect on the decomposition rate was also observed between broad-leaf, but not in secondary forest. These differences in decomposition rate cannot be explained by soil fauna diversity and richness, which often were the most important reasons for fauna effect on decomposition in many other studies (Heneghan et al., 1999a,b; González and Seastedt, 2001). In our study, soil fauna communities in the rain forest were not significantly more diverse

Table 5
Mean decomposition rate (k) for mixed leaf litter in the three forest sites over a period of 360 days.

Sites	2 mm mesh bag (control)		0.15 mm mesh bag (excluded fauna)		Fauna effect (%)
	k	r^2	k	r^2	
Secondary forest	1.075 ± 0.10aA	0.41	0.879 ± 0.04aA	0.74	19.5 ± 1.7A
Broad-leaf forest	1.109 ± 0.10aA	0.51	0.832 ± 0.04bA	0.80	8.7 ± 2.6B
Rain forest	2.123 ± 0.19aB	0.65	0.494 ± 0.10bB	0.57	41.6 ± 1.3C

The regression was of the form $X_t = X_o e^{-kt}$, where X_t is the percentage of the remaining at time t (years), X_o is the initial mass in percent dry weight, and k is the decomposition rate constant.
Different capital letters in a column indicate significance between forest sites with same mesh size. Different small letters within same row indicate significance between treatments (mesh size) at same forest. Results of t-test for paired samples between the two types of litter bags ($n = 10$, $p < 0.05$).

and there were few differences in group and abundance in comparing to the other two sites.

One possible explanation is that the soil fauna play a critical role in the decomposition of leaf litter in tropical rain forest by modifying the initial low N availability and high C/N ratio, which limit microbial activity. The data indicated the soil fauna decrease the C concentration and enhance the N concentration in the rain forest leaf litter, where the initial high C/N ratio is substantially different than initial conditions in the secondary forest and broad-leaf forest (Fig. 2). It is widely recognized that high C/N ratio can restrain microbial decomposition activities (Brown, 1995; Lavelle and Spain, 2001; Tian et al., 1992; Enoki and Kawaguchi, 2000). Soil fauna can enhance N concentration in litter by influencing N release and stimulating microbial N mineralization (Bardgett and Chan, 1999; Heneghan et al., 1999b; González and Seastedt, 2001; Irmler, 2000).

In support of this facilitation by soil fauna for microbial decomposition of leaf litter in the rain forest, our exclusion treatments demonstrated that net N loss was significantly reduced when the macrofauna and the most of mesofauna were excluded. These results consistently support the similar pattern that the relationship between quality and decomposition was most strong in the 0.15 mm smallest mesh bags (fauna excluded treatment), but non-significant in the 2 mm coarsest mesh bags, suggesting a strong interaction between litter quality and soil fauna on decomposition in tropical forests (Smith and Bradford, 2003). Diplopoda (Millipedes) as detritivores and macrofauna which have been experimentally shown to have a significant effect on the mass loss of high C/N ratio litter comparing to low C/N ratio litter (Hättenschwiler and Gasser, 2005). In this study, higher density of Diplopoda in rainy season as compared to dry season in both three forest sites (Table 3), which means they may have more influence on decomposition of mixed litter with high C/N ratio in rain forest site due to increasing N concentration and decreasing C/N ratio (Edwards, 1974; Anderson et al., 1983; Tian et al., 1995; Irmler, 2000; Warren and Zou, 2002). Collembolans, the second most abundant group of fauna in our study, could enhance N mineralization as well (Bardgett and Chan, 1999; Filser, 2002; Xin et al., 2005; Rohan and Richard, 2001). Some groups of Acari, for example the mesotigmatid mites, are very common in tropical wet forest (González and Seastedt, 2001), could provide significant contribution to mass loss (Heneghan et al., 1999a,b). Although the density of Enchytraeidae has been underestimated by Tullgren funnel method for extracting in our study, the difference of Enchytraeidae density among three forest sites implies that this group may have been a factor in that influencing leaf decomposition (Andren et al., 1995), but this still needs more study. Nevertheless, we suspect, the fauna community as a whole, contributed to the adjustment of N concentration and C/N ratio in the litter, especially in the tropical rain forest for which the initial high C/N ratio constrained microbial activities as compared to the litter with low initial C/N ratio in the secondary forest and broad-leaf forest litter.

In conclusion, this study indicated that soil fauna assemblage provided a significant contribution to litter decomposition in all three sites while the contribution of soil fauna to plant litter

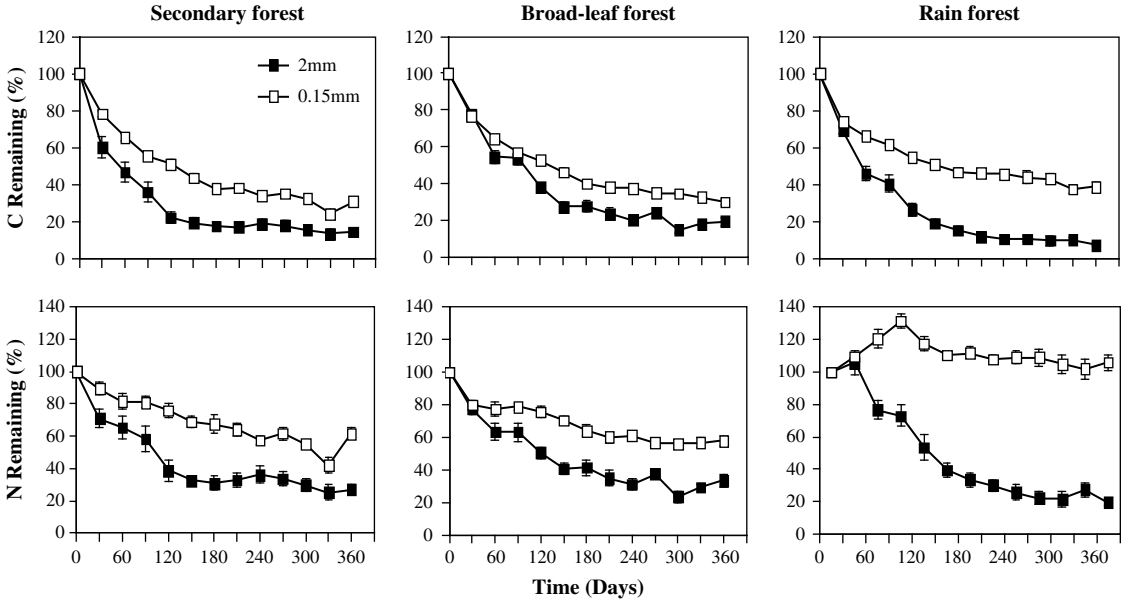

Fig. 2. Changes of absolute amounts of carbon and nitrogen remaining in litter of 2.0 mm and 0.15 mm mesh size litter bags overtime at the three forest sites. (Mean ± SE, $n = 10$.)

decomposition was more pronounced in the rain forest than the other two sites. Fauna effects increased N concentration and decreased C concentration in litter with high initial C/N ratio, which may explain the significant fauna effect on litter decomposition in the rain forest. The research holds implication for the importance of preserving soil fauna diversity in tropical rain forest for the process of nutrient cycling.

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