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Functional redundancy dampens the trophic cascade effect of a web-building spider in a tropical forest floor

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ABSTRACT

The trophic cascade effect of predators on ecosystem functioning is generally believed to be less frequent and weaker in detritus-based than primary producer-based food webs, in part because of functional redundancy among soil fauna. Despite this view, no empirical studies have explicitly examined roles of different soil fauna within trophic levels in mediating cascading effects of predators in detritus food webs. Here we manipulated the density of a dominant funnel-web building spider *Macrothele yunnanica* in permanent plots (1 m^2) for one year. Three spider treatments were applied: 0 spiders, 6 spiders (natural density) and 10 spiders (high density). We found that although changes in spider densities caused large shifts in litter-dwelling Collembola community composition on average, modifying spider densities did not generate a trophic cascade effect and alter litter decomposition in litter bags with coarse mesh (2 mm). Our data supports the hypothesis that functional redundancy among Collembola species may weaken the strength of spider-initiated cascading effects. Consequently, changes in Collembola diversity occupying the same trophic level may not significantly alter ecosystem function in tropical forest-floor ecosystems.

1. Introduction

Generally, increasing diversity of organisms within-trophic group should lead to greater functional redundancy in the ecosystem (Hooper et al., 2005). Functional redundancy in species acts as insurance against environmental fluctuations whereby communities are buffered against the loss of a species such that ecosystem process rates do not change (Yachi and Loreau, 1999; Setälä et al., 2005). Trophic cascades, the indirect effects of predators on non-adjacent trophic levels, have long been recognized in the ecological literature for their strong effects on ecosystem processes (Lawrence and Wise, 2000; Frank et al., 2007; Best and Welsh, 2014). Theoretical and accumulating empirical evidence both suggest that functional redundancy among species may limit the strength of trophic cascades (Borer et al., 2005). For example, in marine ecosystems, as diversity and in turn more potential for functional redundancy among species in the consumer trophic level increases, the intensity of trophic cascades induced by predators are weakened (Frank et al., 2006, 2007; Edwards et al., 2010). In terrestrial food webs, species identity and richness at the herbivore level moderate the cascading effects of predators on plant biomass and ecosystem functioning (Sinclair et al., 2003; Wilby and Orwin, 2013). Compared to knowledge of functional redundancy impacts on trophic cascades in aquatic and above-ground ecosystems, very little is known about detritus-based food webs, especially in tropical soil ecosystems (Gessner et al., 2010; Miki et al., 2014).

Functional redundancy may be a common feature of soil ecosystems (Heemsbergen et al., 2004; Setälä et al., 2005; Miki et al., 2014), and experimental studies manipulating species numbers show an asymptotic response of soil processes, with maximal effects attained with few species (Wardle et al., 1997; Hooper et al.,

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2005). Top-down effects of predators are generally believed to be less frequent and weaker in detritus-based than in primary producer-based food webs (Moore et al., 2004; Wardle, 2006), in part because of functional redundancy among soil fauna; yet this idea has not been tested. Studies on trophic cascades in detritus food webs have focused primarily on the top-down effect among organisms within particular decomposer taxa (e.g., bacteria, nematodes, or protozoa; see reviews by (Moore et al., 2004; Wardle, 2006)), or have focused solely on direct consumers of detritus (e.g., Srivastava et al., 2009).

Empirical evidence and theory suggests that predators have trophic cascade effects on soil ecosystem processes by depressing the densities and species composition of soil fauna in detritus-based food webs (Best and Welsh, 2014; Thakur et al., 2014). One such pathway may involve spiders and Collembola (Lawrence and Wise, 2000; Lensing and Wise, 2006). For example, reducing spider densities could increase rates of decomposition, accompanied by larger Collembola densities in a deciduous forest (Lawrence and Wise, 2000; Lensing and Wise, 2006). Spiders represent a large fraction of the arthropod predator biomass in forest floor ecosystems and spiders are the dominant predators and have high diversity in tropical forest floors (Cardoso et al., 2011). In many detritus food webs, Collembola, an important member of soil mesofauna, have been shown to significantly influence decomposition processes, not only directly as detritivores feeding on organic matter, but also indirectly by altering microbial activities and transporting bacteria and fungal propagules (Fujii and Takeda, 2012; Yang et al., 2012). There is some evidence from soil/litter microcosm studies that litter decomposition was unaffected by varying the number of Collembola species within a trophic group, suggesting that there is considerable functional redundancy in Collembola species (Cragg and Bardgett, 2001; Eisenhauer et al., 2011).

The web-building spider *Macrothele yunnanica* (*Macrothele*, Hexathelidae) is a dominant species with regard to biomass and density in the tropical forest floor of Xishuangbanna, southwest China (Zheng et al., 2009). In this study, we manipulated the densities of *M. yunnanica* in a tropical rainforest floor, and attempted to illustrate: (1) direct effects of *M. yunnanica* density on different Collembola species in a tropical forest floor; (2) trophic cascade effects of *M. yunnanica* on litter decomposition rates; (3) the role of functional redundancy within Collembola group in mediating cascading effects of *M. yunnanica*.

2. Materials and methods

2.1. Study site and spider

Our study was conducted in the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Science (CAS), located in Xishuangbanna, southwestern China (580 m in elevation, 21° 55′ N, 101° 12′ E). This region has a tropical monsoon climate. Mean annual air temperature is 21.5 °C, ranging from 14.8 °C (January) to 25.5 °C (June). The annual mean precipitation was 1557 mm, 85% of which occurs between May and October. The soil type in the study site is red Ultisol. This tropical secondary forest is dominated by 30–50 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 *Gnetum montanum*, *Litsea glutinouse*, *Castanopsis indica*, *Phoebe lanceolata*, and *Schefflera venulosa*.

M. yunnanica can live for about two years and is a dominant spider with regard to biomass and density in this study site (Liu et al., 2014). *M. yunnanica* typically build silk-lined tubular burrow retreats with open “funnel” entrances from which irregular trip-lines radiate over the ground. Usually, they build the funnel-web over crevices in the litter layer of forest floor. *M. yunnanica* stay in their silk-lined tubular burrow retreats. When potential prey contact the trip-lines, the spider rushes out and subdues it by venom injection. This spider is a sit-and-wait predator that has a continuous presence within a fixed habitat location.

2.2. Experimental design

The experiment was conducted for 1 year in fenced plots (1 × 1 m) in our tropical secondary forest study area. The experiment included three spider density treatments: **Spiders excluded:** where all spiders were removed from these plots, thus a negative control; **Six spiders:** where 6 adult *M. yunnanica* spiders were maintained in the plots to mimic local mean density of *M. yunnanica* in this study site; and **Ten spiders:** where 10 adult *M. yunnanica* spiders were maintained in the plots to mimic the highest density of *M. yunnanica* observed in this study site. The reason for the latter treatment is that *M. yunnanica* exhibit obvious temporal and spatial variation in abundances; *M. yunnanica* are not randomly distributed and they can attain high abundances in small patches (about 10 individuals per 1 m^2, S. Liu *personal observation*). Each treatment was replicated 10 times, and all the replicates were randomly deployed in a relatively flat field site (at a minimum spacing between plots of 5 m). For each replicate, fenced plots were enclosed with 80-cm wide iron flashing inserted 20 cm into the ground and covered with 1 mm mesh fiberglass window screen to prevent spiders from entering or escaping. We transferred leaf litter accumulated on these screens back into the plots.

Before starting the experiment, large spiders and other common predators such as carabid beetles, Opiliones and Chilopodes were removed from the plots by hand. Then we carefully sifted all of the litter in each plot through a 5-mm mesh screen *in situ*, removing all remaining spiders and other predators in these plots. All other non-predatory soil fauna were returned to plots. We note that Lawrence and Wise (Lawrence and Wise, 2000) demonstrated that neither sifting litter nor fencing plots influenced rates of leaf litter disappearance. Two weeks later, we released 6 and 10 adult female *M. yunnanica* individuals into the treatment plots designed for Six spiders and Ten spiders, respectively. Spiders were collected locally from our study site. For the duration of this 12-month experiment, we checked each plot 2–3 times per month and if necessary, replenished *M. yunnanica* at the proper treatment densities (electronic supplementary material, Table S1). We did not sift litter again during the experiment.

2.3. Litter decomposition and sampling

We used litterbags to evaluate rates of litter disappearance (Swift et al., 1979). Litter bags were made of 20 × 20 cm polyvinyl with 2.0 mm mesh size. Bags were filled with 10.0 g of air-dried leaf litter. We selected a single species *G. montanum* (leaf litter C:N = 16.6), a dominant plant species in this forest and measured the litter decomposition rates, as an indicator of the potential influence of the spiders. Leaf litter was collected locally from the forest floor of our study area and left to air dry for two weeks before use. Five litter bags were placed below the litter and attached to the ground in each plot. To avoid impacting spider activity, we installed litter bags before adding spiders.

At two-month intervals during the rainy season and three-month intervals during the dry season over the course of a year, one litter bag was randomly retrieved from each plot. After collecting, the litter bags were sealed in a plastic bag and immediately returned to the laboratory. In the lab, we removed litter from litterbags and gently cleaned it of roots, soil and other extraneous materials, and leaf residues were oven-dried at 60 °C until they reached a constant weight to determine the remaining mass.

2.4. Soil fauna sample collection and analyses

To estimate the invertebrate abundance and composition in the plots, we randomly took one 0.0625-m^2 (25 × 25 cm) litter sample from each plot in November 2011 (beginning of experiment), July 2012 (middle of experiment) and December 2012 (end of experiment). Litter samples were placed in cloth bags and loaded into containers cooled with ice packs for transport to the lab. In the lab, soil invertebrates were extracted from the litter samples using Tullgren ("Berlese") funnels for 7 d and collected in 90% ethanol (Edwards, 1991). Fauna were identified to the lowest taxonomic groups according to Yi (2000) and counted under a microscope.

The mesofauna from litter samples were mainly Collembola and Acari, and we identified and sorted Collembola to the genus level: *Onychiurus*, *Neanura*, *Isotoma*, *Entomobrya*, *Sminthurinus*, *Paronellidae*. Although Acari are not potential prey for the spiders we studied (Nentwig, 1987), they were classified into two groups: Oribatida (one of the most abundant groups), and other Acari. We classified the macrofauna to order, and the main orders found were Diplopoda, Diptera larvae, Psocoptera, Coleoptera (adults and larvae), Lepidoptera larvae, Thysanoptera, Pseudoscorpiones, and aggregated the remaining groups (such as Isopoda, Dermaptera, Isoptera, Blattodea and Symphyla) as other macrofauna.

2.5. Statistical analyses

Our analyses followed three steps. First, we identified whether the experimental spider treatments affected Collembola community composition. Next, we identified the effect of experimental treatments on litter decomposition and trophic cascades. Finally, we examined the relationships between Collembola community composition and litter decomposition rates in order to explore the roles of functional redundancy.

To assess the effects of the three spider treatments on the Collembola community in the litter samples, we conducted analyses both at the individual genus and community levels. First, to understand how the abundance of individuals in each genus responded to the spider treatments, we used separate repeated measures Generalized Linear Mixed Models (GLMM) with a Poisson error and a log link function for each genus where plot was treated as a random effect with temporal autocorrelation between samples.

Then, to understand how the community as a whole respond to the spider treatments, we calculated 5 community composition metrics for each plot-total abundance of Collembola, rarefied species richness, Simpson's diversity index, principal components analysis (PCA), and partial constrained redundancy analysis (RDA)—and used these metrics as response variables in the same GLMMs described above. Total abundance per plot was simply the sum of individuals collected in a plot across genera for each sampling time. Due to variation in abundances of individuals across plots and time, we used rarefied species richness (using genera as our species-level taxonomic unit) as our metric of species richness to account for this variation (Gotelli and Colwell, 2010). This metric takes into account the sampling effect, whereby more taxonomic units are found with large sample sizes. We used Simpson's diversity index (Simpson, 1949) as an integrative metric of richness and relative abundance of individuals within each plot. Finally, we used two complementarity ordination methods, PCA and partial constrained RDA, to explore community composition as a whole. We used PCA to explore community composition with respect to the total variation across communities. Partial constrained RDA removes the effect of a conditioning variable from the data (by calculating residuals), and then explores the variation in community composition associated with constraining variables (Pierre Legendre, 2012). We used the amount of litter collected during the three mesofaunal sampling events as the conditioning variable to control for the positive effect of the amount of litter collected on collembolan richness in our data ($P < 0.001$), and the experimental spider treatments and sampling time as the constraining variables. In effect, we used RDA to explore just the variation in community composition due to the spider treatments and sampling time, whereas we used PCA to explore the total variation in community composition that could be caused by any factor. Both PCA and RDA analyses were conducted on the matrix of the relative abundance of individuals in each plot. Rarefied species richness, Simpson's index, PCA and partial constrained RDA were calculated using the vegan library in R (Dixon, 2003).

To understand the effects of the spider treatments and time on litter decomposition in the plots, we again used the same GLMM as described above, with percent mass remaining in the litter bags in each plot at each time point as the response variable. We calculated leaf mass loss rate (K value) in the litter bags over the entire duration of the experiment using Olson's formula (Olson, 1963): $X_t = X_0 \ldots e^{-kt}$, where X_t is mass remaining at time t, X_0 was mass at $t = 0$, and k is annual mass loss rate. We used one-way ANOVA analyses to test the effects of experimental treatments on the annual decomposition rate. Log-transformations were employed when the data did not meet the assumptions of normality.

Finally, to understand how Collembola community composition influenced litter decomposition throughout the experiment, we used linear regression with percent mass lost at the end of the experiment as the response variable, and the mean community composition over time for each metric as the independent variables.

3. Results

3.1. Spider treatment effects on Collembola and macrofauna community

In our litter samples, we identified a total of 6 Collembola genera. Repeated-measure GLMMs showed that spider treatments had a significant effect on the abundance of all Collembola genera (all $P < 0.05$, Table 1). Tukey honest significant difference (HSD) *post hoc* tests indicated that the abundance of *Onychiurus* in the 10 spiders treatment was significantly lower than that under the spider excluded and 6 spiders treatment ($P = 0.003$, $P = 0.001$, respectively), and there were no differences between the spider excluded and 6 spiders treatments ($P = 0.85$) (Fig. 1A). Compared with spider excluded treatments, the density of *Entomobrya* was lower in 10 spiders treatment ($P = 0.03$) (Fig. 1D). In contrast, *Isotoma* and *Sminthurinus* abundance was higher in 10 spiders treatment compared to the spider excluded treatment ($P = 0.04$, $P = 0.01$, respectively) (Fig. 1C, F). *Neanura* abundance was lower in 6 spiders treatment than the spider excluded treatment ($P = 0.02$) (Fig. 1B). We observed no differences in abundance of *Paronellidae* (all $P > 0.50$) (Fig. 1E). For the Acari group, which was not potential prey of these spiders, there were no significant differences among the three spider treatments (All $P > 0.05$, electronic supplementary material, Table S2).

We calculated 5 community-level metrics to assess how the Collembola community changed in response to the spider treatments and sampling time. The total abundance of Collembola in plots and Simpson's diversity index were not affected by the experimental treatments or sampling time (Table 2, Fig. 2). Rarefied species richness exhibited a significant treatment by sampling time interaction ($P < 0.05$, Table 2), due to the samples in the 10 spiders

Table 1
Summary of the repeated measures GLMMs used to test for effects of treatment, sampling period and their interaction term on the abundance of different Collembola taxa.

Source	*Onychiurus*		*Neanura*		*Isotoma*		*Entomobrya*		*Paronellidae*		*Sminthurinus*	
	Wald x^2	*df*	Wald x^2	*df*	Wald x^2	*df*	Wald x^2	*df*	Wald x^2	*df*	Wald x^2	*df*
Treatment (T)	23.78^{**}	2	9.36^{*}	2	7.07^{*}	2	7.76^{*}	2	7.09^{*}	2	13.22^{**}	2
Sampling period (S)	13.00^{**}	2	25.63^{**}	2	8.88^{*}	2	10.42^{*}	2	0.98	2	8.80^{*}	2
T × S	3.05	4	3.00	4	1.59	4	5.32	4	1.49	4	14.02^{**}	4

($^{*}P = 0.05$, $^{**}P = 0.01$, and $^{***}P = 0.001$).

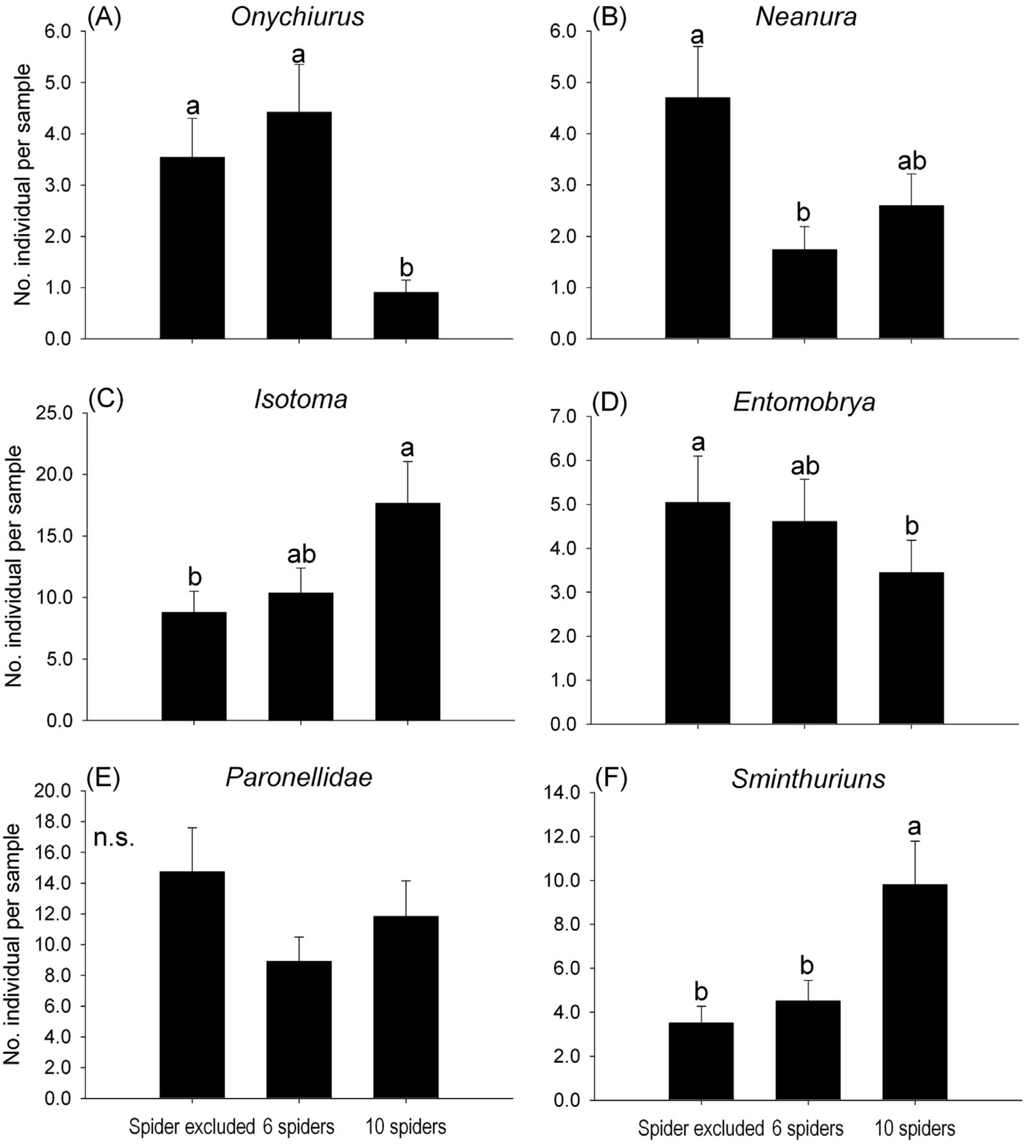

Fig. 1. Effects of different spider treatments on the density of main groups of Collembola in litter samples. (A) *Onychiurus*, (B) *Neanura*, (C) *Isotoma*, (D) *Entomobrya*, (E) *Paronellidae*, (F) *Sminthurinus*. Data are expressed as mean ± s.e. Means with different letters are significantly different ($P < 0.05$) and n.s. indicates no significance ($P > 0.05$). Note that *y*-axes have different scales.

treatment increasing in rarefied species richness across the sampling times (Fig. 2B). In our PCA, the first three axes explained 66.0% of the variation in community composition. The first PCA axis (PC1) explained 25.3% of the variation and exhibited a significant treatment by sampling time interaction ($P < 0.05$, Table 2) due to the spider excluded treatment having a low PC1 value in the first sample (Fig. 2D). The second axis (PC2) explained 21.2% of the variation and was significantly correlated with treatment ($P < 0.05$, Table 2). The third axis (PC3) explained 19.5% of the variation and was weakly correlated with sampling time ($P < 0.1$, Table 2). *Sminthurinus* and *Entomobrya* were positively associated with PC1, all genera except *Paronellidae* and *Entomobrya* were positively associated with PC2, and *Isotoma* and *Entomobrya* were positively associated with PC3 (electronic supplementary material, Fig. S1).

In our partial constrained RDA, the constrained (treatment and sample time) and conditioned (leaf litter amount) variables

Table 2
Summary of the GLMMs used to test for the effects of treatment, sampling period and their interaction on the community composition metrics.

	Treatment		Sampling period		Treatment × sampling period	
	Wald x^2	*df*	Wald x^2	*df*	Wald x^2	*df*
Abundance	1.45	2	0.04	1	0.55	2
Rarefied species richness	0.44	2	0.46	1	6.51^*	2
Simpson's diversity index	0.04	2	0.74	1	5.87^+	2
RDA1	2.86	2	13.26^{**}	1	2.60	2
RDA2	18.06^{**}	2	0.67	1	1.62	2
PC1	1.66	2	0.48	1	7.43^*	2
PC2	7.77^*	2	0.32	1	4.10	2
PC3	3.36^+	2	3.83	1	1.69	2

($^+P < 0.1$; $^*P < 0.05$; $^{**}P < 0.01$).

together explained 18.3% of the variation in community composition. The overall RDA was significant ($F_{3,\,81} = 2.98$, $P < 0.01$), as were spider treatment ($F_{2,\,81} = 1.98$, $P < 0.05$) and sample time ($F_{1,\,81} = 4.97$, $P < 0.01$). The first RDA axis (RDA1) explained 59% of the constrained variation, and was not associated with spider treatment ($P = 0.24$), but was significantly associated with sampling time ($P < 0.001$, Table 2) with later samples having higher RDA1 values (Fig. 2E). The second axis (RDA2) explained 27% of the constrained variation and was significantly associated with the spider treatments ($P < 0.001$, Table 2), but not sampling time ($P = 0.41$), with the spiders excluded treatment having significantly higher RDA2 values than the 6 spider treatment (Fig. 2F). All genera except *Isotoma* and *Sminthurinus* were positively associated with RDA1 suggesting the relative abundances of *Isotoma* and *Sminthurinus* were affected more than the other genera in earlier samples (electronic supplementary material, Fig. S1). Comparatively, all genera except *Onychiurus* were positively associated with RDA2, suggesting that the relative abundance of *Onychiurus* was affected by the spider excluded treatment (Fig. S1). Note, because PC2 and RDA2 were significantly associated with spider treatment, and PC3 and RDA 1 were associated with sample time, we elected to report the results for all analyses in the tables, however, only displayed the patterns for the stronger relationships, RDA1 and RDA2, in figures.

For the macrofauna group, there were no significant differences among the three spider treatments except for Thysanoptera (electronic supplementary material, Fig. S2).

3.2. Trophic cascade effects of spider on litter decomposition

We initiated the experiment with 5 litter bags per plot, however, due to some plots being destroyed by falling trees, we were not able to assess litter decomposition and related soil fauna community in one of the plots under 6 spiders treatment and two of plots under 10 spiders treatment. We observed significant decomposition in our litter bags over the course of our experiment as indicated by increasing percent mass lost over time ($F_{2,\,4} = 23.32$, $P < 0.01$, Fig. 3A). However, there was no effect of spider treatment on the percent of mass lost over the course of the experiment ($F_{2,\,4} = 0.97$, $P = 0.46$, Fig. 3B), percent of mass lost at the end of the experiment ($F_{2,\,23} = 0.76$, $P = 0.48$), or mean annual decay rate (K value) ($F_{2,}$

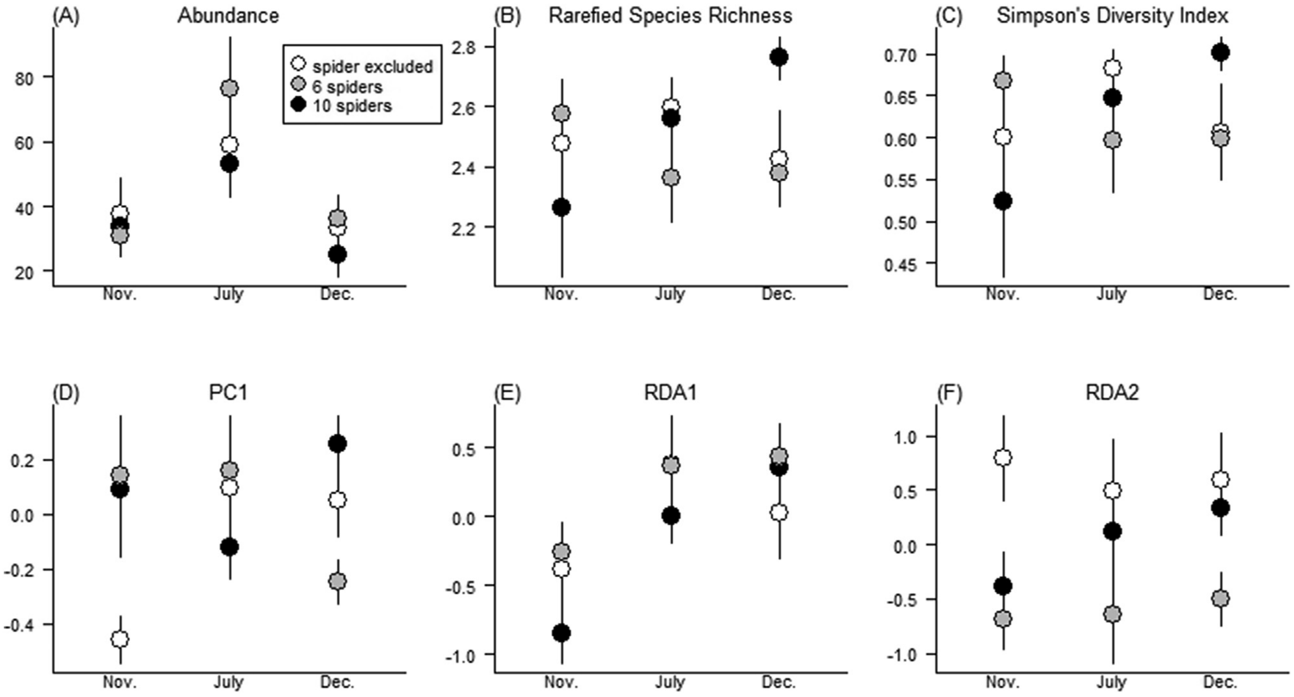

Fig. 2. Means ± se of community composition metrics—total Collembola abundance (A), rarefied species richness (B), Simpson's diversity index (C), PC1 (D), RDA1 (E), and RDA2 (F)—for each treatment over the three sampling time periods (November 2011, July 2012, and December 2012). Significance of relationships listed in Table 2.

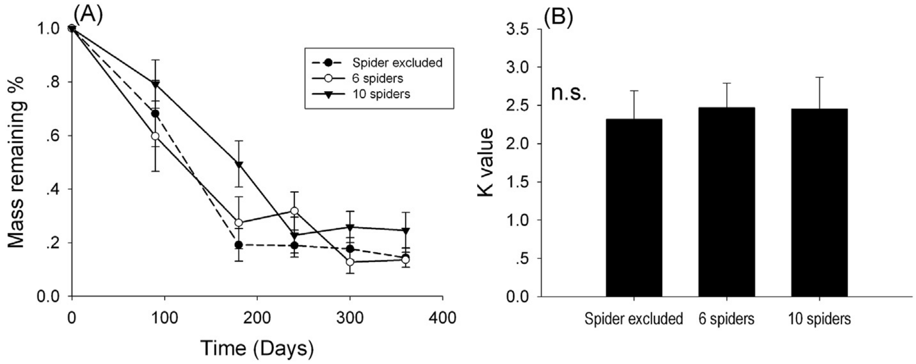

Fig. 3. Changes in the mass remaining of litter in the litter bags among the three spider treatments over a period of 360 days (A). Effects of different spider treatments on the annual mean decomposition rate (K value) (B). Data are expressed as mean ± s.e., and n.s. indicates no significance ($P > 0.05$).

Table 3
Results of ordinary least squares regressions showing power of community composition metrics to explain variation in percent mass lost at the end of the experimental period.

Explanatory variable	Coefficient	*P*	R^2
Abundance	−0.001	0.35	0.037
Rarefied species richness	−0.018	0.85	0.001
Simpson's diversity index	−0.149	0.60	0.012
PC1	0.021	0.79	0.003
PC2	−0.035	0.63	0.010
PC3	−0.140	0.17	0.079
RDA1	−0.066	0.20	0.067
RDA2	0.028	0.38	0.033

$_{24} = 0.05$, $P = 0.96$) (Fig. 3B), showing that spider density treatments had no trophic cascade effects on litter decomposition.

3.3. *Effects of collembolan community composition on mass loss of litter*

In other words, although community composition changed throughout the course of the experiment, litter decomposition was not affected by these changes. Although our 5 community composition metrics showed considerable variation, and some of that variation was explained by sampling time and spider treatment, none of the metrics explained the variation of the percentage of mass loss at the end of the experiment (All $P > 0.05$, Table 3, Fig. 4).

4. Discussion

In this study, we found that although changes in the density of a predatory spider had varying effects on different Collembola genera, which in turn altered community composition, there were no cascading effects on litter decomposition. Our data suggest that the Collembola communities appear to be capable of maintaining litter decomposition via compensatory responses, thus buffering the impact of spider predation. Furthermore, functional redundancy is likely to exist among other soil fauna taxa which also can influence pathways of litter decomposition and nutrient dynamics.

4.1. *Spider treatment effects on different Collembola species*

In our study, high density spider treatment (10 spiders) significantly decreased the abundance of two genera, *Onychiurus* and *Entomobrya*, but increased the abundance of two other genera, *Isotoma* and *Sminthurinus*. As a result, our ordination analyses revealed the community in the 10 spider treatment was predominantly *Isotoma* and *Sminthurinus*, whereas the other four genera comprised the communities in the 6 spiders and spider excluded treatments. Other work from similarly species-rich aquatic and aboveground ecosystems have also shown this pattern where the suppression of preferred prey species may be compensated for by increased production of less preferred prey species (Edwards et al., 2010; Wilby and Orwin, 2013). The large shifts in abundance in these groups likely indicate differential susceptibility to predators.

In our study system, *Entomobrya* are active in the litter layer on the forest floor, while our study spider, *M. yunnanica*, is sit-and-wait predator. An early study predicted that sit-and-wait predators were more likely to encounter and consume mobile prey (Scharf et al., 2011), which likely explains why the 10 spider treatment had lower abundance of *Entomobrya*. In contrast, *Isotoma* species are less mobile in the litter layer (Bilde et al., 2000), and hence were less conspicuous to *M. yunnanica*. Other factors that might affect prey choice include vertical stratification of different Collembola species within the soil affecting encounter rates with spiders (Faber and Joosse, 1993), for instance, *Isotoma* are largely epigeic and *Onychiurus* are soil dwelling. In addition, Collembola species have different nutrient composition and toxic substances, which could affect spider consumption capacity. Possible chemical defenses have been reported for some families of Collembola (Hopkin, 1997; Agusti et al., 2003).

4.2. *Trophic cascade effects of spider on litter decomposition*

The annual mean decomposition rate (K value) across these three spider treatments was not significantly different, indicating that spider treatments had no cascading effects on decomposition. Our findings are consistent with previous work which found that spiders did not indirectly change litter decomposition rate (Miyashita and Niwa, 2006). In a previous spider-density experiment, we did not detect trophic cascades in litter bags with coarse mesh (2 mm), but recorded them in litter bags with fine mesh (1 mm) (Liu et al., 2014). Possible explanation for the different responses of the two mesh size (2 mm and 1 mm) is that macrofauna community and microclimatic differences between litter bags of different mesh sizes might oppose the effect of soil arthropods on litter decomposition (Bokhorst and Wardle, 2013; Frouz et al., 2015).

Our findings agree with previous work (Cragg and Bardgett, 2001) which found that changing the number of species of Collembola within a trophic group has no predictable effect on litter decomposition, suggesting functional redundancy in Collembola communities with respect to litter decomposition (Gessner et al.,

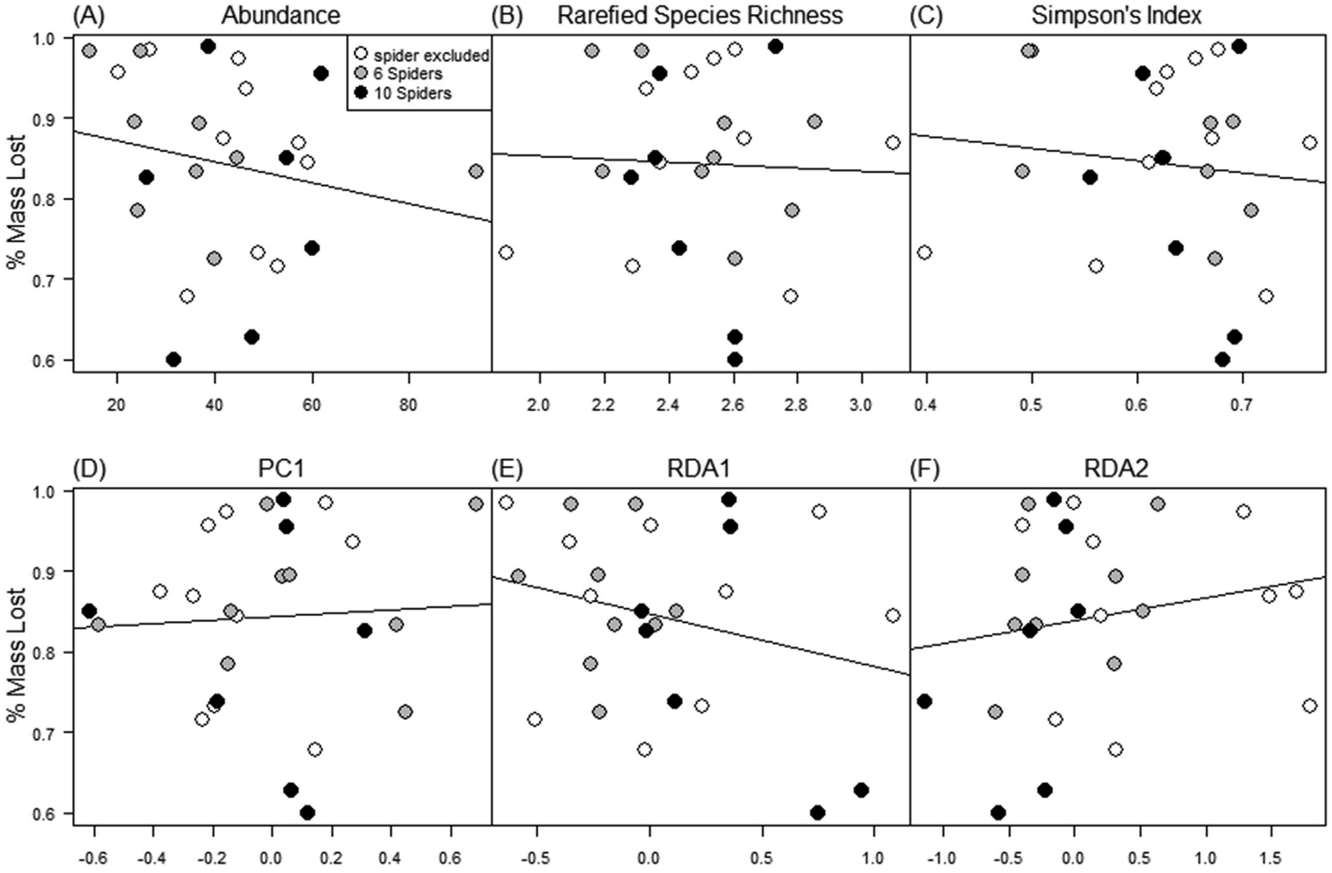

Fig. 4. Effect of the Collembola community composition metrics—total Collembola abundance (A), rarefied species richness (B), Simpson's diversity index (C), PC1 (D), RDA1 (E), and RDA2 (F)—on percent mass lost at the end of the experiment. Data points are plot means across three time periods, and lines are the best fit regression lines corresponding to analyses reported in Table 3.

2010). This conclusion is also supported by an experiment that used eight detritivore species from different taxonomic groups and found no influence of species richness on litter decomposition (Heemsbergen et al., 2004). Consequently, our study suggests that redundancy among Collembola within the same trophic level dampens the trophic cascade effect of spiders.

Collembola appear to be generalist feeders using a great diversity of resources (Hopkin, 1997; Endlweber et al., 2009), and nitrogen stable-isotope work has assigned Collembola to three feeding guilds (Chahartaghi et al., 2005). In addition, there is evidence that some Collembola species may switch their diets in response to the presence of other Collembola species (Chahartaghi et al., 2005). These findings suggest that niche overlap among Collembola species results in functional redundancy. This may explain why in our study, the high density spider treatment did not have cascading effect on litter decomposition even though it dramatically changed Collembola community composition. Although the overall density of *Onychiurus* and *Entomobrya* was lower than the density of *Sminthurinus* and *Isotoma*, previous studies indicated that Collembola species composition was a better predictor for litter decomposition than Collembola species density (Cragg and Bardgett, 2001; Eisenhauer et al., 2011). This may be because interspecific interactions between Collembola species, such as competition and facilitation, may affect litter decomposition (Eisenhauer et al., 2011).

4.3. *Conclusion*

Our study showed that although spider treatments changed Collembola community composition, these change did not cascade into changes in litter decomposition in litter bags with coarse mesh (2 mm), which is consistent with functional redundancy. Soil fauna diversity can enhance food web complexity when functional redundancy among soil fauna exists. Food web complexity is thought to weaken the strength of detritus trophic cascades (Kadoya and McCann, 2015). Consequently, changes in Collembola diversity may not significantly alter ecosystem function in tropical forest-floor ecosystems.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.soilbio.2016.03.020.

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