



Cascading effects of spiders on a forest-floor food web in the face of environmental change

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Abstract

Spiders have cascading effects on forest-floor food webs and ecosystem processes by depressing soil fauna densities and altering species composition. However, it remains unclear how spiders with different foraging strategies influence cascading effects on decomposition. In addition, prolonged droughts would likely have important consequences for trophic interactions in detritus-based food webs. In the present study, we evaluated how interactions between spider predation and drought affect litter decomposition in a tropical forest floor. We manipulated densities of dominant spiders with actively hunting or sit-and-wait foraging strategies in microcosms which mimicked the tropical-forest floor. We found a positive trophic cascade on litter decomposition rates triggered by actively hunting spiders under ambient and reduced moisture. However, sit-and-wait spiders showed no cascading effects on litter decomposition under ambient and drought conditions. Our findings suggest that trophic interactions in detritus-based food webs should be considered to better understand litter decomposition in the face of environmental change.

Zusammenfassung

Spinnen üben Kaskadeneffekte auf die Nahrungsnetze des Waldbodens und Ökosystemprozesse aus, indem sie die Siedlungsdichten der Bodenfauna reduzieren und die Artenzusammensetzung ändern. Es bleibt indessen unklar, wie Spinnen mit unterschiedlichen Beuteerwerbsstrategien die Kaskadeneffekte auf die Streuzersetzung beeinflussen. Darüber hinaus sollten ausgedehnte Trockenperioden deutliche Konsequenzen für die trophischen Interaktionen in streubasierten Nahrungsnetzen haben. Wir untersuchten, wie die Interaktionen zwischen Räuberdruck durch Spinnen und Trockenheit die Streuzersetzung in einem tropischen Waldboden beeinflussen. Wir manipulierten die Dichten von dominanten aktiv jagenden bzw. lauernden Spinnenarten in Mesokosmen, die den tropischen Waldboden nachahmten. Wir fanden sowohl bei Umgebungsbedingungen als auch bei reduzierter Feuchte einen positiven trophischen Kaskadeneffekt auf die Zersetzung, der durch die aktiv jagenden

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Spinnen ausgelöst wurde. Die Lauerjäger zeigten dagegen keine Kaskadeneffekte. Unsere Ergebnisse legen nahe, dass solche trophischen Interaktionen für ein besseres Verstehen der Streuzersetzung angesichts von Umweltveränderungen berücksichtigt werden sollten.

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Introduction

The forest floor is a complex and dynamic biological system in which macro-, meso-, and micro-invertebrates occur together with microorganisms and collectively influence key soil processes (Ohta, Niwa, Agetsuma, & Hiura 2014; Potapov, Semenyuk, & Tiunov 2014). Free-living predators, such as spiders, salamanders, ground beetles inhabit the forest floor, playing key roles in regulating populations of other soil fauna, and thus have indirect effects on ecosystem functions such as litter decomposition and primary productivity (Best & Welsh 2014; Cardoso, Pekar, Jocque, & Coddington 2011; Zhao, Griffin, Wu, & Sun 2013). For instance, Best and Welsh (2014) demonstrated that woodland salamanders suppressed some invertebrate taxa, therefore increased leaf litter retention and facilitated carbon capture in a northern California forest. Spiders represent a large fraction of arthropod predator biomass in forests-floor ecosystem and previous studies have found that spiders have cascading effects on forest-floor food webs (Lawrence & Wise 2000, 2004; Liu, Chen, He, Hu, & Yang 2014; Miyashita & Niwa 2006), but no general pattern of effects has emerged. Lawrence and Wise (2000) and Liu et al. (2014) found that litter decomposition rates were reduced in field enclosures with spiders in comparison to spider-absent control enclosures, a finding attributed to predation on Collembola by spiders. In contrast, Lawrence and Wise (2004) reported that spiders accelerated decomposition rates. Miyashita and Niwa (2006) showed that reduced spider abundance increased Collembola density, but it did not change litter decomposition rates.

Some differences among findings are likely to derive from different foraging strategies of spiders among studies. Foraging strategies of spiders, whether actively foraging or sit-and-wait predators, may determine their ability to suppress soil fauna densities by shaping the probability of encountering prey (Schmitz 2008, 2009). Scharf, Lubin, and Ovadia (2011) predicted that sedentary prey were more likely to be captured by widely foraging predators, while sit-and-wait predators were more likely to encounter and consume mobile prey. Therefore, predator foraging strategy could be a key functional trait explaining variation in cascading effect of spiders in detrital food webs (Miller, Ament, & Schmitz 2014; Schmitz 2008).

Precipitation is another factor that has not been investigated adequately with regard to detrital spider–food-web interactions, but which can be an important determinant of

the strength of trophic cascade effects in detritus-based food webs (Lensing & Wise 2006). Meanwhile, droughts could become more frequent and intense in Yunnan, southwestern China, which might be caused by the El Niño/Southern Oscillation (ENSO), an atmospheric circulation system that originates in the western Pacific Ocean and brings rainfall to Southeast Asia (Qiu 2010). Changes in precipitation amounts can directly alter soil moisture which strongly influences soil fauna reproduction and development rates (Waagner, Bayley, & Holmstrup 2011). Furthermore, drought can directly modify soil fauna community composition and abundance by altering soil microclimate, and indirectly by altering resource availability and composition of the soil food web (de Vries et al. 2012; Kardol, Reynolds, Norby, & Classen 2011). Therefore, a prolonged drought period may affect the sign of spider-induced cascading effect in detritus-based food webs.

Here we report on an experiment examining the effects of spiders with two different foraging strategies, actively hunting (AH) and sit-and-wait (SW), on invertebrate densities and decomposition rate of leaf litter. We conducted an experiment in microcosms mimicking the tropical rainforest floor ecosystem to test the following hypotheses: (1) sit-and-wait spiders could be more likely to encounter and consume mobile soil fauna, while actively hunting spiders could consume the majority of soil fauna; (2) thus actively hunting spiders may have stronger cascading effects than sit-and-wait spiders on litter decomposition rates; (3) drought influences the direction of spider-induced cascades in detritus-based food webs.

Materials and methods

Studied spiders

The sit-and-wait spider, *Macrothele yunnanica* (Hexathe-lidae) can live for about two years at a fixed habitat location. It thus may provide a persistent point-source cue of high risk to prey (Scharf et al. 2011). These spiders build silk-lined tubular burrow retreats with open funnel entrances from which irregular trip-lines radiate over the litter layer. The actively hunting spider, *Pardosa laura* (Lycosidae) can live for about eight months, and roams widely on the forest floor in search of prey. *M. yunnanica* and *P. laura* are dominant spiders with regard to biomass and density in this study site (Liu et al. 2015). The study system consists of spiders, Collembola and

Acari, where Collembola are potential prey of spiders, but Acari are not prey for the spiders we studied (Appendix A: Fig. 1).

Experimental set-up

We conducted the experiment in microcosms (diameter 60 cm, height 20 cm). Microcosms were prepared in plastic pots and filled with 25 kg of fresh-weight-equivalent soil and 250 g fresh litter and humus from a tropical secondary forest located in Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences (101°11' E, 21°56' N). Soils were sieved through 5-mm mesh to remove rocks and roots and then thoroughly homogenized. The soil was an oxisol, with a soil organic matter content of 39 g kg⁻¹ and total N of 2.29 g kg⁻¹. Litter and humus were collected from the same site as the soil samples. After collections, litter was carefully sifted through a 3-mm mesh screen, removing all spiders encountered, as well as twigs and rocks. All non-spider fauna were put back and then the litter was fully mixed. This litter and humus hosted the ambient faunal community at natural level populations. Microcosms were covered with 1-mm mesh fiberglass screen to limit migration of spiders and soil fauna. All microcosms were kept in the same tropical secondary forest floor throughout the experiment. To each microcosm, we added leaf litter every month to match the natural monthly litter fall flux (Appendix A: Table 1). That litter was collected from the same forest by suspended litter traps, and fauna were removed from it by a freeze–thaw cycle. More detailed descriptions of geomorphology, vegetation and soil in our study site can be found in Liu et al. (2015).

Experimental design

The experiment began in March 2012 and ended in April 2013. Microcosms were placed on the forest floor in a randomized block design with 10 treatment blocks. Each block, consisting of one replicate per treatment, had at least 5 m spacing. Within blocks, we randomly divided the microcosms into two rainfall treatments: ambient or drought. Four microcosms in each block were uncovered and received natural rainfall (ambient treatment). Rain shelters, 1.5 m above the microcosms, were constructed over the four drought microcosms using PVC pipes and transparent polyethylene sheeting. The roofs over four microcosms excluded rainfall to simulate severe drought conditions (drought treatment), but allowed natural ventilation. Then we randomly assigned microcosms in each block to one of four spider treatments: Control: where no spiders were added; SW spiders: where 4 adult female *M. yunnanica* spiders were maintained in the microcosms; AH spiders: where 4 adult female *P. laura* spiders were kept in the microcosms; SW + AH spider: where 2 adult female *M. yunnanica* and 2 adult female *P. laura* spiders were kept in the microcosms. These densities were slightly

higher than the range (*M. yunnanica*: 2–12 individual/m², average value 6 individual/m²; *P. laura*: 1–9 individual/m², average value 6 individual/m²) observed in the field. Spiders were collected locally from this forest. During this one-year experiment, we checked spider abundances two or three times per month and replenished them when needed (Appendix A: Table 2).

Litter decomposition

We used litterbags to evaluate the rates of litter mass loss (Swift, Heal, & Anderson 1979). Litter bags were made of 10 cm × 10 cm polyvinyl with 1.0 mm mesh. Bags were filled with 3.0 g dry leaves from *Pometia tomentosa* (leaf litter C: $N = 42.5 \pm 3.18$), a dominant plant species in the forest. Leaves were collected locally from the same forest and were air dried for two weeks before use. We used a brush to clear extraneous materials and soil fauna from leaf litter. Six litter bags were set below the litter and attached to the soil surface in each microcosm. To avoid impacting spider activity, we installed litter bags before adding spiders.

Sample collection and analysis

To determine initial densities of soil fauna in the microcosms, we collected a 0.01-m² (10 cm × 10 cm) litter sample from each microcosm before the spiders were added. One litter sample was taken from a random location from each microcosm at the beginning of the experiment in March 2012. The soil fauna were extracted from the litter samples using Tullgren (“Berlese”) funnels for 7 d and collected into 90% ethanol (Edwards 1991). Fauna were identified to taxonomic groups according to Yi (2000) and counted under a microscope.

Litter bags were randomly retrieved from each microcosm at two-month intervals. After collecting, the litter bags were sealed into a cloth bags and immediately returned to the laboratory. In the lab, all soil fauna from the litter bags were extracted by Tullgren funnels into 90% ethanol (Edwards 1991). After extraction, we gently removed roots, soil and other extraneous materials. Leaf residues were oven dried at 60 °C until they reached constant weights to determine the remaining mass.

Invertebrates from litter bag samples were mainly Collembola and Acari, and we identified and sorted Collembola to the genus level: primarily *Entomobrya* and *Paronellinae*. We aggregated *Sminthurinus*, *Onychiurus*, *Isotoma*, and *Neanura* into Other Collembola. We identified and sorted Acari to Oribatida and Other Acari, but Acari are not potential prey for the spiders we studied (Nentwig 1987).

Soil moisture in microcosms was measured monthly at 0–5 cm depths using a FieldScout® TDR 300 (Spectrum Technologies Inc., USA).

Statistical analysis

First, we performed one-way ANOVA to detect differences in initial densities of soil fauna among treatments. To account for multiple comparisons, we used Bonferroni adjusted *P*-values to test for differences among spider treatments. We used a repeated measures Generalized Linear Mixed Model (GLMM) analysis with a Poisson error and a log-link function to compare responses among taxonomic groups (Collembola and Acari). The independent variables included in the analysis were spider treatment, rainfall, block and sampling period. In this analysis, microcosm was treated as a random effect with temporal autocorrelation (first-order autoregressive process) between samples. The Generalized Linear Mixed Models were performed with SPSS statistical software ver. 20.0 using the GENLIN procedure. Quasi-likelihood models were used to deal with overdispersion.

Leaf mass loss rate (*k*) from the litter bags 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. There were 10 replicates for *k*-value determinations. We estimated the strength and sign of trophic cascades as: trophic cascade index = $(k_{\text{spider}} - k_{\text{control}})/k_{\text{control}}$, where k_{spider} means *k*-value in either SW, AH or SW + AH treatment and k_{control} means *k*-value in the control treatment (Lensing & Wise 2006). We then used two-way ANOVA to test the effects of spider treatment, rainfall (drought and ambient treatments) and their interaction terms on trophic cascade index.

We used repeated measured ANOVA to examine the soil moisture differences between ambient and drought microcosms.

Results

Initial density of soil fauna communities and soil moisture

Initial soil faunal densities among the four treatments used for natural and reduced rainfall manipulations did not differ (all *P*>0.05) (Appendix A: Table 3). The rainfall shelters limited water input to microcosms and reduced soil moisture ($F=272.08$, *P*<0.001) (Appendix A: Fig. 2).

Comparison of soil fauna abundance among different spider treatments under ambient and drought conditions

Repeated-measure GLMMs showed that interactions between spider and rainfall treatments had significant effects on the abundance of various soil fauna (all Collembola *P*<0.05) (Table 2), thus we separately compared these groups under drought and ambient conditions. The taxonomic groups of Collembola responded differently to spider

Table 1. The abundance of Acari (not potential prey of these spiders), from litter bags among four treatments under drought and ambient conditions (Mean ± s.e.m., *n* = 10).

Rainfall	Treatment	Oribatida	Other Acari
Drought	SW + AH	8.51 ± 1.32ab	6.35 ± 0.54a
	SW	10.29 ± 1.56ab	7.31 ± 0.65a
	AH	13.74 ± 2.04a	7.58 ± 0.65a
	Control	7.47 ± 1.16b	5.79 ± 0.48a
Ambient	SW + AH	17.03 ± 2.49ab	10.71 ± 0.82a
	SW	14.55 ± 2.14ab	9.63 ± 0.74a
	AH	23.52 ± 2.42a	9.28 ± 0.71a
	Control	15.63 ± 2.30b	9.60 ± 0.73a

Different letters in a column indicate significance among different treatments, at *P*<0.05. AH = actively hunting spiders, SW = sit-and-wait spiders.

treatments. Under ambient conditions, *Entomobrya* abundance was lower in SW + AH compared to control treatment (all spiders excluded, as below) (*P*=0.04), and there were no differences among other spider treatments and control (all *P*>0.05) (Fig. 1A). The spider treatments significantly reduced *Paronellinae* abundance compared to the control (SW + AH: *P*=0.01, SW: *P*=0.035, AH: *P*=0.04) (Fig. 1B). We observed no differences in abundance of Other Collembola across the four treatments under ambient conditions (all *P*>0.50) (Fig. 1C). Higher abundance of Total Collembola was found in control than in SW + AH treatment (Fig. 1D).

For the Acari group, we unexpectedly found that AH treatment had the highest Oribatid abundance compared to the control treatment under drought and ambient condition (*P*=0.03, *P*=0.04, respectively) (Table 1). However, there was no effect of spider treatments on Other Acari (All *P*>0.05, Table 1).

Under drought conditions, the AH treatment had higher *Paronellinae* abundance than SW + AH, SW or control treatments (*P*=0.02, *P*=0.02, *P*=0.03, respectively) (Fig. 1B). The same pattern occurred for Total Collembola (Fig. 1D). We observed no differences in abundance of *Entomobrya* and Other Collembola across the four treatments (Fig. 1A and C).

In addition, repeated-measure GLMMs showed that interactions between sampling period and spider treatments had significant effects on soil fauna abundance (all Collembola *P*<0.05) (Table 2), which indicates that spider treatments develop differently over time (Appendix A: Fig. 3). Furthermore, SW × AH interactions for *Paronellinae* (Wald $\chi^2=16.75$, *P*<0.001) and total Collembola (Wald $\chi^2=14.55$, *P*<0.001) were significant, indicating that SW + AH treatment effects were intermediate to separate SW and AH treatments (Appendix A: Table 5).

Effects of drought on soil fauna abundances across the four spider treatments

Among Collembola, drought significantly decreased the abundance of Total Collembola compared with ambient

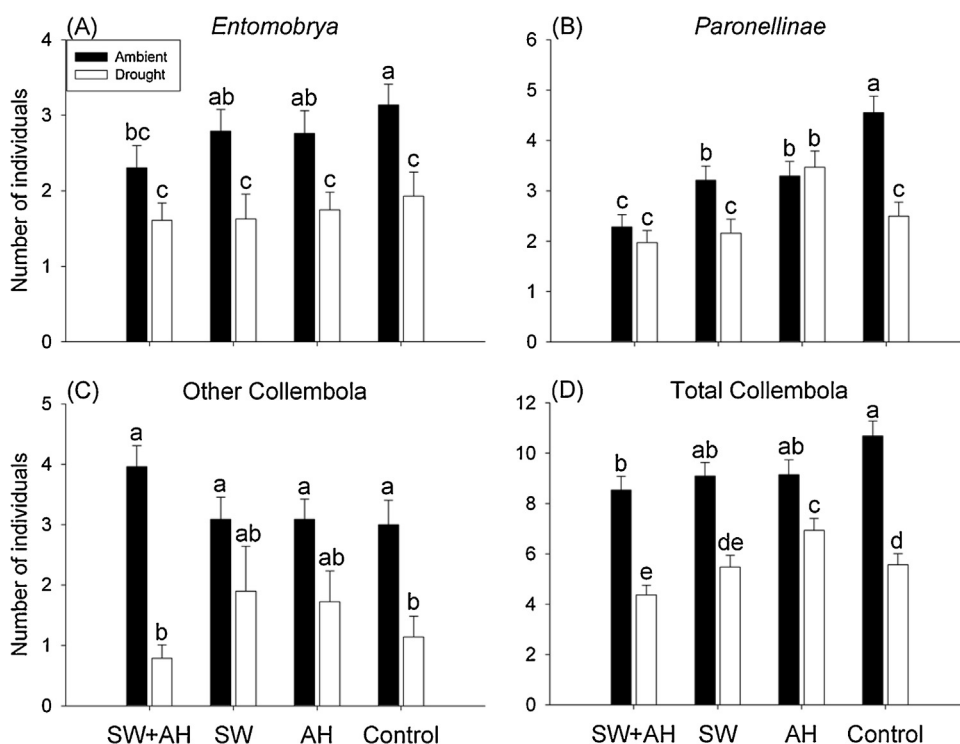


Fig. 1. Effects of different spider treatments on abundances of the main groups of Collembola under ambient and drought conditions. (A) *Entomobrya*, (B) *Paronellinae*, (C) Other Collembola, (D) Total Collembola. Data are expressed as mean $\pm$ s.e.m. ($n = 10$). Means with different letters are significantly different ($P < 0.05$). Note that y-axes have different scales.

treatment across all spider treatments (Fig. 1D). For *Entomobrya*, drought had significant effects in three treatments other than SW + AH ($P < 0.01$) (Fig. 1A), and drought had significant effects on *Paronellinae* in SW and control treatments as opposed to the other two (Fig. 1B). The abundance of other Collembola was significantly higher in ambient microcosms than in drought microcosms under SW + AH treatment and control ($P = 0.01$, $P = 0.006$, respectively) (Fig. 1C) (see more detail in Fig. 1).

Decomposition rate and trophic cascade index

Drought significantly decreased decomposition in our litter bags ($F = 136.75$, $P < 0.001$, Fig. 2). Spider treatments also had significant effects on mass loss over the course of the experiment ($F = 3.97$, $P = 0.039$, Fig. 2).

Spider treatments ($F = 6.57$, $P = 0.001$) and rainfall ($F = 3.61$, $P = 0.01$) had significant effects on trophic cascade index (Appendix A: Table 4). A positive trophic cascade

Table 2. Summary of repeated measures GLMMs used to test the effects of spider treatment, rainfall (drought and ambient treatments) and sampling period, and their interaction terms on the abundance of different soil fauna taxa ($n = 10$).

Source	<i>Entomobrya</i>		<i>Paronellinae</i>		Other Collembola		Total Collembola	
	Wald χ^2	df	Wald χ^2	df	Wald χ^2	df	df	df
Block (B)	62.73***	9	79.32***	9	60.06***	9	68.96***	9
Sampling period (S)	446.55***	5	316.30***	5	478.13***	5	682.63***	5
Treatment (T)	16.17*	3	27.45**	3	22.28**	3	31.56**	3
Rainfall (R)	15.57*	1	16.03*	1	37.76**	1	75.49***	1
T $\times$ S	44.99***	15	87.63***	15	22.97**	15	72.99***	15
T $\times$ R	10.17*	3	17.35*	3	25.28**	3	24.13**	3
R $\times$ S	26.77*	5	202.90***	5	94.64***	5	141.96***	5
T $\times$ R $\times$ S	29.90*	15	89.67***	15	22.89**	15	118.30***	15

* $P = 0.05$.

** $P = 0.01$.

*** $P = 0.001$.

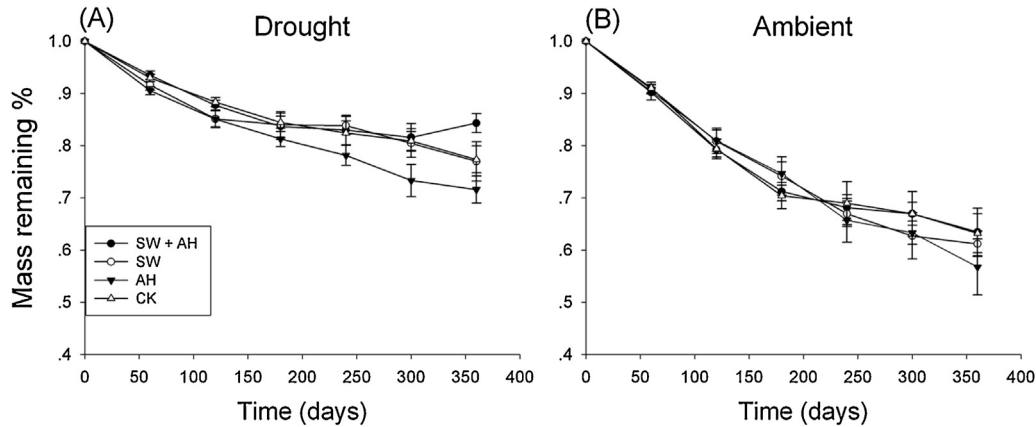


Fig. 2. Changes in the mass remaining of litter in the litter bags among the four spider treatments under drought (A) and ambient (B) condition over a period of 360 days. Data are expressed as mean $\pm$ s.e.m. ($n = 10$).

index (above the dotted line) indicates positive treatment effects on litter decomposition, a value near the dotted zero line indicates the absence of trophic cascades, and a value below zero indicates negative treatment effects on litter decomposition rates (Fig. 3). Under ambient moisture conditions, the cascade indices of SW+AH and SW were close to zero ($P = 0.39$; $P = 0.28$, respectively), indicating no cascading effect on decomposition rates (Fig. 3). In contrast, AH significantly accelerated decomposition rates ($P = 0.04$). Under drought conditions, SW+AH treatments reduced decomposition rates ($P = 0.04$), but AH accelerated decomposition rates ($P = 0.005$), and SW had no cascading effect on litter decomposition ($P = 0.64$) (Fig. 3). The P -values in Fig. 3 indicate differences in trophic cascade index between ambient and drought conditions. Results comparing trophic cascade indices in ambient and drought among the spider treatments showed that the cascading effect in ambient microcosms was higher than in drought microcosms under SW+AH spider treatments ($P = 0.046$). There were no differences between ambient and drought microcosms under the SW and AH treatments ($P = 0.20$ and $P = 0.44$, respectively).

Discussion

In this study, we found a positive trophic cascade on litter decomposition rates triggered by actively hunting spiders under ambient and drought moisture, which could be explained by their indirect beneficial effects on Oribatid abundance. However, sit-and-wait spiders had no cascading effects on litter decomposition under ambient or drought conditions.

One possible explanation for indirect beneficial effects of spiders on oribatids is that mobility of Acari is very low, between 1 and 5 cm/day (Berthet 1964), thus they are unlikely to encounter sit-and-wait spiders. Chemical defenses of Acari may also reduce attacks by actively hunting spiders (Nentwig 1987). This is consistent with previous findings that the presence of salamanders (*Desmognathus eschscholtzii*) decreased densities of *Entomobryidae* springtails and adult

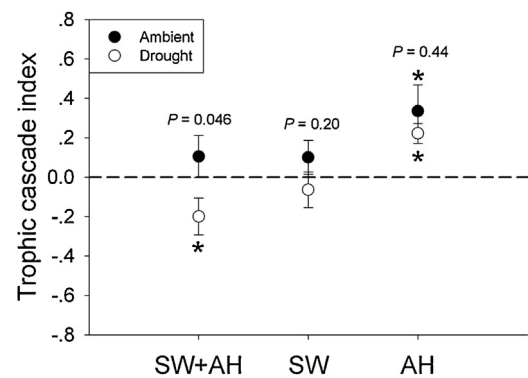


Fig. 3. Spider-induced trophic cascade effects on leaf litter decomposition rate under ambient and drought conditions expressed as trophic cascade index. A trophic cascade index significantly >0 indicates positive effects of treatments on litter decomposition, an index value significantly <0 indicates negative effects of treatments on litter decomposition. Asterisks (*) indicate significance differences between index and dotted line (zero) ($P < 0.05$). Data are expressed as mean $\pm$ s.e.m. ($n = 10$). The P -values indicate significance of differences in trophic cascade index between ambient and drought conditions.

beetles, while increasing the density of oribatid mites (Best & Welsh 2014). The removal of these two soil invertebrates by salamanders probably opened up resources for the smaller and more numerous mites, allowing their increase (competitive release) (Best & Welsh 2014). Oribatid mites can increase litter mass loss by stimulating microbial respiration rates, altering microbial extracellular enzymes, and other transformations of litter chemistry (Wickings & Grandy 2011). In this study, the AH spider treatment had higher Oribatid density compared with the control treatment under ambient and drought conditions. Therefore, actively hunting spiders had a positive trophic cascade on litter decomposition rates. Lawrence and Wise (2004) also found that wandering spiders enhanced decomposition.

In our study system, *Entomobrya* and *Paronellinae* were active in litter on the forest floor. An earlier study predicted

that predators were more likely to encounter and consume mobile prey (Scharf et al. 2011), which likely explains why the three spider treatments had lower abundance of *Paronellinae*. In contrast, some other Collembola, such as *Sminthurinus* and *Neanura* species often have small furcae that ease their movement in the litter layer (Bilde, Axelsen, & Toft 2000), and hence were less conspicuous to spiders. Other factors that might affect prey choice include vertical stratification of different Collembola species within the soil affecting encounter rates with spiders (Faber & Jooisse 1993). In addition, Collembola species have different nutrient composition and toxic substances, which could affect spider predation. Possible chemical defenses have been reported for some families of Collembola (Hopkin 1997; Agustí et al. 2003).

Although we found evidence that SW spiders significantly decreased the abundance of *Paronellinae* and total Collembola compared to the control treatment under ambient condition, we did not detect significant cascading effects in the sit-and-wait spiders treatment under ambient moisture. Soil fauna represent multiple trophic roles and their functional diversity influences decomposition in complicated ways (Frouz, Roubickova, Hedenec, & Tajovsky 2015). *Paronellinae* may not act as primary decomposers and their functions could be replaced by other Collembola species, weakening intensity of trophic cascades. Under drought, the SW treatment did not show a cascading effect on leaf litter decomposition rate. This is reasonable as the density of Collembola in SW treatment was not different from those in control treatment. In contrast, the SW + AH spider treatment had a significant negative trophic cascade index under drought condition, and this is understandable as the density of total Collembola in the SW + AH spider treatment was lower than in the control treatment.

The trophic cascade indices in SW and AH spider treatments under drought were not significantly different from the indices under ambient moisture. Although densities of total Collembola and *Entomobrya* under drought were lower than those under ambient condition, previous studies indicated that Collembola species composition was a better predictor for litter decomposition than Collembola species density (Cragg & Bardgett 2001; Eisenhauer, Sabais, & Scheu 2011). This may be because interspecific interactions between Collembola species, such as competition and facilitation, may affect litter decomposition (Eisenhauer et al. 2011). Our findings are consistent with Lensing and Wise (2006) in that altering rainfall did not consistently affect the cascading index.

In our previous spider-drought experiment, we observed negative trophic cascade effects on litter decomposition in SW and AH spider treatments under drought conditions and drought reversed the cascading effects of spiders on litter decomposition rates (Liu et al. 2015). However, in our previous study, we used coarse-mesh litter bags (2 mm), while we used fine-mesh (1 mm) bags in the present experiment. The possible explanation for the different responses between mesh sizes (2 mm and 1 mm) is that microclimatic differences

between litter bags of different mesh sizes might oppose the effect of soil arthropods on litter decomposition. In addition, most macrofauna can enter the larger-mesh but not the fine-mesh bags. This may be another possible reason for these different results.

Conclusions

Our study revealed that different spider-foraging strategies had different trophic cascade effects under drought and ambient moisture. Furthermore, reduced soil-moisture content decreased the abundance of soil fauna, but did not change the trophic cascade effect of spiders in a tropical forest floor. As a consequence, understanding how increased dry periods affect roles of soil biota in ecosystem processes such as litter decomposition and nutrient return to forests is important for predicting the responses of tropical forest-floor to global climate change.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.baae.2016.03.004>.

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