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Nitrogen addition changes the trophic cascade effects of spiders on a detrital food web

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Abstract. The trophic cascade effects of predators on detrital food webs have crucial impacts on ecosystem functioning. However, due to the complexity of detrital food webs, no consistent pattern of cascading effects has emerged. Furthermore, global changes, such as increased nitrogen (N) deposition, likely have significant impacts on detrital trophic interactions but are not well understood. Here, we evaluate how increased N deposition influences trophic cascades using a simplified detrital food web (spider–Collembola) that has previously exhibited trophic cascades in an experimental context. We tested the impact of N addition on the direct and cascading effects of spiders in detritus food web. We manipulated the abundance of spiders with sit-and-wait or actively hunting foraging strategies in microcosms. Under ambient N conditions (control treatments), we did not detect trophic cascade effects of spiders on litter decomposition. In contrast, N addition enhanced the negative trophic cascade effects of spiders on decomposition by directly reducing Collembola density. Our findings suggest that understanding how increased N deposition affects trophic interactions and ecosystem functioning is important for predicting the impact of global change on soil ecosystems.

Key words: Collembola; detritus food webs; litter decomposition; nitrogen deposition; spiders; trophic cascade effect.

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INTRODUCTION

Ecologists have long recognized the importance of top-down effects in structuring the herbivore community and ecosystem functioning in terrestrial ecosystems (Schmitz 2008, Schmitz et al. 2010, Hawlena et al. 2012). Top-down effects of predators can propagate through the food web to influence changes in primary producers or other lower trophic levels, resulting in a trophic cascade (Schmitz 2008, Carpenter et al. 2010, Schmitz et al. 2010). Trophic cascades are the most familiar example of top-down indirect effects (Schmitz 2008, Carpenter et al. 2010, Schmitz et al. 2010). Trophic cascades, reciprocal predator–prey effects that alter changes of nonadjacent trophic level, are mostly demonstrated for aboveground ecosystems (Schmitz 2008, Carpenter et al. 2010, Schmitz et al. 2010). In contrast, the role of trophic cascade effects in detrital food webs has been less explored. Understanding how cascading effects are mediated by soil predators may improve our knowledge of trophic interactions in detritus-based food webs (Strickland et al. 2013, Liu et al. 2014, 2016*b*).

In detrital food webs, different trophic levels including primary decomposers, secondary decomposers, omnivores, and top predators occur together and collectively influence key soil functions and processes (Fitter et al. 2005, Bardgett and van der Putten 2014). Increasing evidence indicates that predators can directly depress soil arthropod densities and change species composition, thereby triggering trophic cascade effects on ecological processes in detrital food webs, such as leaf litter decomposition rates and carbon exchange (Laakso and Setala 1998, Setala 2002, Best and Welsh 2014). However, no consistent patterns of cascading effects on detrital food webs have emerged, and previous studies have produced a range of results from positive (Lawrence and Wise 2004) to negative (Liu et al. 2014), to no effects (Miyashita and Niwa 2006) on soil animal densities or litter decomposition. These highly variable results illustrate the complexity of detrital food webs (Liu et al. 2016*a*).

Shifts in detritus trophic interactions due to global change may be a key factor influencing the strength of trophic cascades in detrital food webs, yet this has not been well investigated, especially nitrogen (N) deposition (Gan et al. 2013). In China, atmospheric N deposition has increased dramatically due to rapid industrial, agricultural, and urban development (Liu et al. 2011, 2013). Most of the deposited N will eventually end up in the soil, potentially changing the abundance and composition of soil fauna by altering soil conditions, such as soil pH and carbon storage (Xu et al. 2006, 2009). Shifts in soil fauna composition in response to N deposition can significantly slow litter decomposition rates and decrease the flux of nutrients entering the detrital food web (Niu et al. 2016). However, it is not known how N deposition and potential feedbacks could influence trophic cascades in simplified spider–Collembola detrital food webs. Based on these lines of evidence, we hypothesized that N deposition may change the strength of trophic cascade effects by reducing Collembola abundance.

In detrital food webs, the trophic cascades involving spiders and Collembola have been demonstrated experimentally in many forest ecosystems (Lawrence and Wise 2004, Liu et al. 2014, 2016*b*). Forest floor spiders are key predators, representing a large proportion of predator abundance and biomass in detrital food webs, and previous empirical evidence indicates that spiders have top-down effects on soil ecosystem function by decreasing soil biota abundance in detritus-based food webs (Liu et al. 2014, 2015, 2016*b*). However, the effects of spiders on soil biota may depend on the spider foraging strategies (Schmitz 2008, Liu et al. 2015). Generally, spiders can be divided into two guilds based on foraging strategies: actively hunting (AH) spiders and sit-and-wait (SW) spiders. AH spiders decrease prey densities directly by consuming them, but SW can also cause behavioral changes in prey which reduces prey foraging rates (Schmitz 2008, Liu et al. 2015). In terrestrial detrital food webs, Collembola, an important component of soil meso-fauna, are a significant prey source for spiders, and also play a significant role in decomposition processes by feeding on plant litter and stimulating microbial activities (Chahartaghi et al. 2005). Following Schmitz (2008), we hypothesized that AH spiders with actively foraging strategies would be more effective at suppressing Collembola densities than SW spiders, because AH spiders directly decrease prey density (density-mediated effect), whereas SW spiders induce predator-avoidance behavior in the prey (trait-mediated effect).

We examined how simulated N deposition influences the trophic cascade effects of spiders on leaf litter decomposition by experimentally manipulating the abundance of spiders with two foraging strategies, sit-and-wait (SW) and actively hunting (AH), in microcosms with Collembola. The specific objectives were to test: (1) Whether the two spider types have different direct effects on Collembola abundance, and whether spider–Collembola interactions cascade to affect litter decomposition; (2) whether nitrogen addition affects the spider–Collembola interaction with cascading effects on litter decomposition. We predict negative trophic cascade effects of spider–Collembola interactions on litter decomposition, and the cascading effects of spiders on decomposition would be strengthened by N addition.

METHODS

Microcosm setup

This study was conducted in microcosms (plastic pots: diameter 27 cm, height 30 cm) in a temperature-controlled greenhouse (20°C; 70% humidity; 12-h illumination). We collected soil and litter from a tropical secondary forest located at the Xishuangbanna Tropical Botanical Garden

(XTBG), Chinese Academy of Sciences (101°11′ E, 21°56′ N), and frozen at −22°C for two weeks to eliminate all soil fauna (Huhta et al. 1989), and inspections of the material after freezing confirmed soil fauna were eliminated. Microcosms were filled to a height of 10 cm with 3 kg (fresh weight) of sieved (5 mm) and homogenized soil with a layer of 16 g of leaf litter on top to mimic the forest floor ecosystem. Fresh leaf litter was collected from same site as soil samples. The fresh litter was composed mainly of *Pometia tomentosa*, *Litsea glutinosa*, *Castanopsis indica*, *Phoebe lanceolata*, and *Schefflera venulosa*. The litter was fully mixed and air-dried before use. The soil was an oxisol, with a soil carbon content 39.0 g/kg, N content 2.3 g/kg, and pH 4.4. All microcosms were covered with fiberglass screen (mesh size = 1 mm) to prevent the escape of spiders and Collembola.

Focal spider and Collembola species

Pardosa laura (Lycosidae) and *Macrothele yunnanica* (Hexathelidae) are dominant spider species in the lowland tropical forest floor ecosystems at our study site at XTBG (Liu et al. 2016*b*) and exhibit different foraging strategies. *P. laura* is an active hunting predator that actively searches for prey on the forest floor with a lifespan of about eight months. *M. yunnanica* is web-building, sit-and-wait predator and with a lifespan of about two years and typically builds a funnel web in the litter layer (see more detailed descriptions in Liu et al. 2016*b*).

Seira delamarei Jacquemart 1980 (Collembola: Entomobryidae) is a dominant Collembola species in our tropical forest study site, and is a primary decomposer feeding on litter and detritus (Chahartaghi et al. 2005). Our previous studies found that this Collembola species was a main potential prey of spiders in this system (Liu et al. 2014, 2016*b*). The lifespan of *S. delamarei* is about two months.

Experimental design

The experiment began in January 2011 and ended in June 2011. The experiment included 2 nitrogen treatments (ambient and N-addition) × 4 spider treatments (no spider control, SW spiders, AH spiders, and SW + AH spider treatment) × 6 replicates, producing a total of 48 microcosms. We used a randomized block design with six treatment blocks. Within blocks, we randomly assigned the microcosms to the two nitrogen treatments: nitrogen addition or ambient. On 3 January 2011, the N-addition microcosms were sprayed with 15 mg N per microcosm as solutions of NH_4NO_3 (about 26 g N/m^2, 0.3 L solution per microcosm, a rate approaching expectations of increased N input in South China; Liu et al. 2013). Our objective was to make the total N concentration in the N-addition microcosms was double the concentration in the ambient N microcosms. Following N-addition, 130 medium-sized adult *S. delamarei* (Collembola) from laboratory cultures were added to each of the microcosms. Subsequently, medium-sized female adult spiders were added to the following spider treatments: (1) control (no spiders added, CK), (2) two SW spider individuals (SW), (3) two AH spider individuals (AH), and (4) one SW spider individual + one AH spider individual (SW + AH). These spider densities were within the range observed in the field (*M. yunnanica*: 2–12 individuals/m^2, average value: 6 individuals/m^2; *P. laura*: 1–9 individuals/m^2, average value: 6 individuals/m^2). During this six-month experiment, the microcosms were checked weekly and spider abundances were replenished when needed (Appendix S1: Table S1).

Litterbag sampling and decomposition

We used litterbags to examine litter decomposition in the microcosms (Swift et al. 1979). We enclosed 3.0 g of air-dried *Phoebe lanceolata* (C: N ratio = 26.1) leaf litter into 8 × 8 nylon mesh bags (mesh size 1.0 mm) and placed three bags on the soil surface of each microcosm. *Phoebe lanceolata* is a dominant plant species at our study site, and newly fallen leaves of *P. lanceolata* were collected from the forest floor. To avoid impacting Collembola and spider activity, the litter bags were added before the Collembola and spiders.

Litterbags were sequentially retrieved from each microcosm (at 40, 100, and 180 days) over the course of experiment. After collecting, Collembola were removed from the litterbags using a brush and returned to the microcosms. We then gently cleared adhering soil particles and other extraneous material from leaf residues. Leaf residues in the bags were oven-dried at 60°C until they reached constant weights to determine the remaining mass.

Collembola sampling and analyses

We used bait sampling methods to estimate the *S. delamarei* abundance in the microcosms at 40, 100, and 180 days over the course of the experiment (Joseph and Bettiga 2016). Thin slices (~0.5 cm thick) of potato (5 cm diameter) as Collembola bait were placed on the surface of the litter in each microcosm. After 24 h, bait slices were collected and returned to the laboratory and the number of *S. delamarei* on the bait slices was quantified under a microscope within 24 h of collection. After counting, the *S. delamarei* were returned to their original microcosms.

Statistical analyses

To determine the influence of spiders and N treatments on Collembola abundance, we used a repeated-measures ANOVA with spider and N treatments as main effects and block was treated as a random effect. We used independent *t* tests to compare soil pH, NH_4^+, and NO_3^- concentrations between ambient and N addition treatments under each spider treatment at the end of experiment.

Leaf mass loss rate (k) from the litter bags was estimated 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. There were six replicates for k value determinations. Two-way ANOVA was performed to examine the effects of N treatment, spider treatment, and their interaction on the k value, with block included as a random effect.

We calculated the trophic cascade effect size in both the ambient and N added treatments using the trophic cascade index. The index is calculated as index = $(k_{\text{spider}} - k_{\text{control}})/k_{\text{control}}$, where k_{spider} represents k value (decomposition rate) in either AH, SW, or SW+AH treatment, and k_{control} represents k value in the no spider treatment (control treatment; Lensing and Wise 2006). To test for the effects of spider treatments, nitrogen addition, and their interaction terms on the cascading index, we used two-way ANOVA. To account for multiple comparisons, we used Tukey's HSD post hoc test to evaluate the difference in cascading indices among spider treatments. All data analyses were conducted with SPSS software version 20.0 (SPSS, Chicago, Illinois, USA).

Results

Nitrogen addition effects on soil pH, NH_4^+, and NO_3^- concentrations

Soil pH was reduced by N addition, from 5.32 to 5.02 ($t = 15.02$, $P < 0.001$; Table 1). The N addition increased soil inorganic N concentrations, with an 89.55% increase in soil NH_4^+ ($t = 19.63$, $P < 0.001$) and a 141.87% increase in soil NO_3^- ($t = 25.32$, $P < 0.001$; Table 1).

Direct effects of nitrogen addition and spider treatments on Collembola abundance

The spider treatments ($F = 12.21$, df = 3, $P < 0.001$), the N treatments ($F = 11.02$, df = 1, $P = 0.002$), and their interaction ($F = 3.08$, df = 3, $P = 0.039$) all significantly impacted Collembola abundance (Table 2). AH spiders significantly reduced Collembola abundance more than SW spiders, while N addition reduced Collembola abundance relative to the ambient treatments (Fig. 1). The significant interaction between spider and N treatments was due to higher Collembola abundance in the SW treatment than the AH treatment under ambient conditions; however, under the N addition treatment, Collembola

Table 1. Comparisons of soil parameters in ambient and N addition treatments (mean ± SE, $n = 24$).

Resource	pH	NH_4^+ (mg/kg)	NO_3^- (mg/kg)
Ambient	5.32 ± 0.02	165.42 ± 2.78	32.70 ± 1.27
N addition	5.02 ± 0.04**	313.56 ± 7.02**	79.09 ± 1.32**

** $P < 0.01$.

Table 2. Results of the repeated-measures ANOVA for effects of N addition, spider treatments, and their interaction on the Collembola abundance, *Seira delamarei* ($n = 6$).

Source	df	Collembola *F*	Collembola *P*
Within-subjects effects			
Time	3	76.45	0.000
Time × Spider treatment	9	0.74	0.676
Time × N	3	7.35	0.000
Time × Spider treatment × N	9	1.71	0.095
Between-subjects effects			
Spider treatment	3	12.21	0.000
N	1	11.02	0.002
Spider treatment × N	3	3.08	0.039

abundance was highest in the control treatment and lowest in the AH treatment (Fig. 1).

Cascading effects of spider treatments on litter decomposition

N addition significantly reduced litter decomposition in litter bags ($F = 86.25$, $P < 0.001$, Fig. 2), as did the spider treatments ($F = 5.20$, $P = 0.02$, Fig. 2). N addition reduced the litter decomposition rate (k value; $F = 12.68$, $P = 0.001$, Appendices S1: Table. S2).

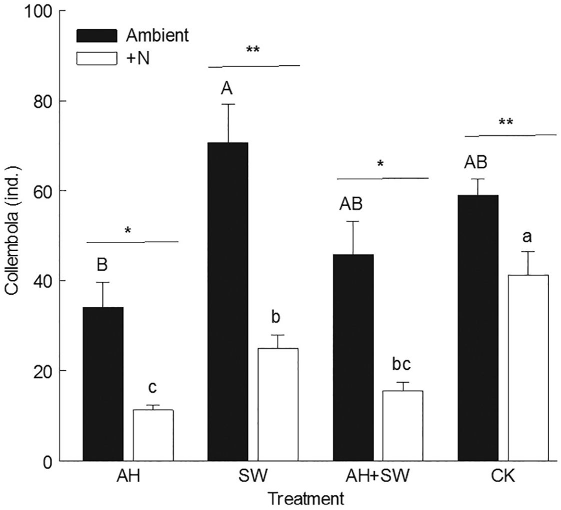

Fig. 1. Impact of spider treatments on Collembola abundance under N addition and ambient conditions. Values are mean ± SE. Different capital letters indicate significant difference among spider treatments under ambient conditions, and different small letters indicate a significant difference under N addition conditions ($P < 0.05$). Asterisks (*) indicate a significant difference between N addition and ambient conditions within the same spider treatments (*$P < 0.05$, **$P < 0.01$).

The trophic cascade index revealed that the trophic indices of all three spider treatments were close to zero under ambient conditions (SW: $P = 0.89$; AH: $P = 0.78$, SW + AH: $P = 0.55$, respectively), suggesting absence of cascading effects on litter decomposition (Fig. 3). In contrast, under N addition conditions, all three spider treatments had negative trophic cascade index values (SW: $P < 0.001$; AH: $P = 0.027$, SW + AH: $P < 0.001$, respectively) indicating reduced litter decomposition rates (Fig. 3). Comparing trophic cascade indices between the ambient and N addition treatments for each spider treatment showed that N addition microcosms had consistently stronger cascading effects than ambient microcosms across all three spider treatments (SW: $P = 0.007$; AH: $P = 0.05$; SW + AH: $P = 0.033$, respectively, Fig. 3).

DISCUSSION

We found that spiders, irrespective of foraging strategies, indirectly reduced litter decomposition rates but only under N addition conditions, which was likely due to the combined effect of spiders and N reducing Collembola abundance. Because the N addition reduced Collembola abundance, N itself exhibited an effect on litter decomposition equal to that of a trophic cascade. Together, the combined effects of N and spider predators on

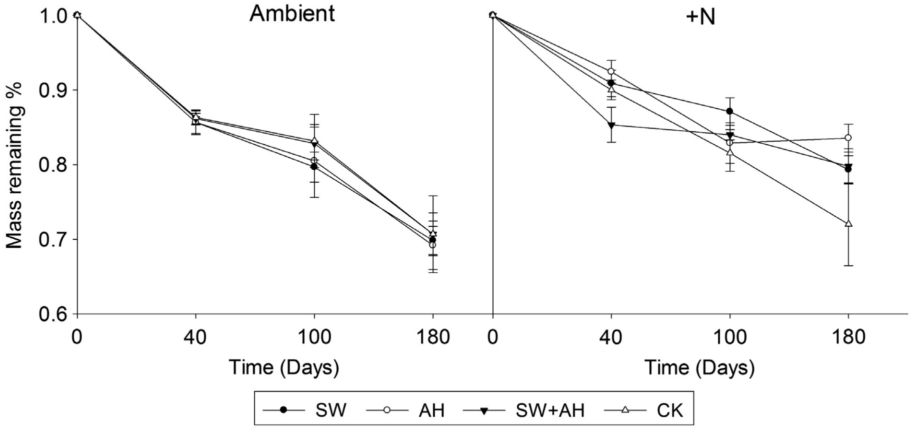

Fig. 2. Changes in the mass remaining of litter in the litter bags among the four experimental treatments over a period of 180 days. Data are expressed as mean ± SEM.

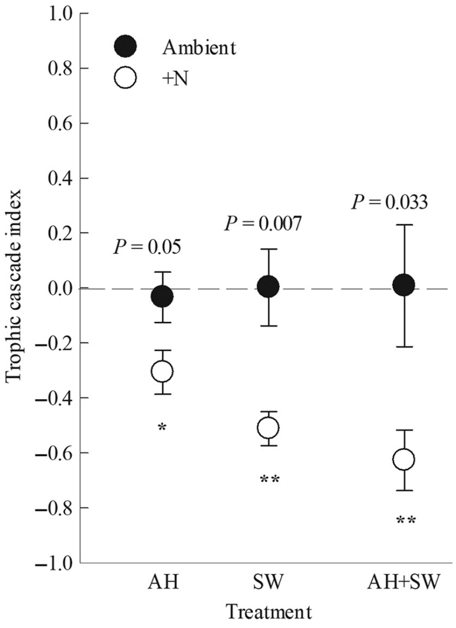

Fig. 3. The effects size of spider trophic cascade on litter decomposition under N addition and ambient condition (mean ± SEM, $n = 6$). The trophic cascade index is significant if the error bars do not overlap dashed line (zero) shown by the asterisks ($^{*}P < 0.05$, $^{**}P < 0.01$). Trophic cascade index above the zero (dashed) line indicates positive cascading effect (treatments enhanced litter decomposition); index intersecting zero line indicates absence of cascading effect; and index below dashed line indicates negative effect (treatments reduced litter decomposition). The P values denote the differences in cascading index between N addition and ambient conditions.

Collembola abundance triggered significant reductions in litter decomposition and subsequent trophic cascades. Our negative cascading effects of spiders agree with previous results that show the presence of spiders could decrease decomposition rates, due to decreases in Collembola density (Lensing and Wise 2006, Liu et al. 2014).

Nitrogen addition changes cascading effects of spiders

The trophic cascade index in all three spider treatments under N addition was lower than the index under ambient conditions, suggesting that N addition significantly decreased the strength of trophic cascade. N addition significantly decreased Collembola abundance compared to the ambient condition in all spider treatments. Numerous studies have shown that N inputs could lead to soil acidification (Xu et al. 2006, 2009, Gan et al. 2013), and soil acidification can cause serious declines in Collembola abundance in soil ecosystems (Xu et al. 2006, 2009). In our experiment, pH was lower in N addition microcosms, which may have reduced Collembola abundance. Previous work has indicated that even small changes in soil pH, comparable to what we observed in our study, impact Collembola species growth and development, reproduction, fecundity, and longevity (Salmon et al. 2002). Therefore, N addition enhanced the negative trophic cascade effects of spiders on decomposition by directly reducing Collembola abundance.

Trophic cascade effects of spider treatments on decomposition

Under ambient conditions, Collembola abundance did not differ across the three spider treatments and control treatments, which caused no cascading effects on litter decomposition rate. One possible reason is that Collembola density was high, and spiders consumed the proportion of the Collembola population that would have suffered natural mortality in the absence of predation (Riechert and Lockley 1984). Another possible reason is that these spiders cause largely evasive behavioral responses (non-lethal effect) in their Collembola prey (Schmitz 2008). This result is inconsistent with our previous findings, which showed the cascading effect of spider treatments on litter decomposition (Liu et al. 2014). However, it is notable that the experimental design and food webs differed substantially between the current and previous studies; the previous study was conducted in 1 × 1 m field plots that included more components of the forest floor ecosystem compared to the simplified food webs in microcosms used in the current study. Because the previous study more closely mimicked natural conditions, we anticipate the impact of N deposition on trophic cascades to be even stronger in those conditions, yet this remains to be tested.

Spider foraging strategies dominate the Collembola suppression

In this study, our results are consistent with hypotheses that AH spiders have higher predation rates on Collembola than SW spiders. Previous results have demonstrated that AH spiders have strong lethal effects (density effects) on prey density but cause little habitat shift, whereas SW spiders cause habitat shifts in prey without significant lethal effects (Schmitz 2008, Schmitz et al. 2010). Empirical evidence has shown that SW predators cause largely anti-predator behavioral responses (e.g., evasive behavior) because prey species respond strongly to persistent, point-source cues of predator presence, and actively foraging AH predators may reduce prey density, but they present highly variable predation risk cues (Schmitz 2008, Schmitz et al. 2010). This may explain why AH spiders appear to be more effective at reducing Collembola abundance than SW spiders. In addition, *S. delamarei* have furcae, which could help them be less conspicuous to sit-and-wait predators.

CONCLUSIONS

In summary, our study demonstrates that changes in N concentration can impact the trophic cascade effects of spiders in the detritus-based food web by changing densities of Collembola. Furthermore, spider foraging strategies had different impacts on Collembola suppression. We show that increased N deposition affects the strength of trophic cascade effect in tropical soil ecosystem by altering nonadjacent trophic interaction. Understanding the impacts of pollution on species interactions is important for predicting the impact of global climate change on tropical soil ecosystems.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2466/full