# 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.

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## 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.,

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