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Trophic cascade of a web-building spider decreases litter decomposition in a tropical forest floor

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ABSTRACT

Trophic cascade effects on detritus-based food webs of forest floor have the potential to alter ecosystem functioning, but due to the complexity of detrital food web no general pattern of cascading effects has emerged. The goal of this study was to evaluate trophic cascade effects of a dominant funnel-web building spider on leaf-litter decomposition rate and microbial biomass in a tropical forest floor. 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 spider, 6 spiders (natural density) and 10 spiders (high density). We found that the high density of *M. yunnanica* led to significant negative cascading effects on litter decomposition rate, which is probably due to decreased density of one dominant collembolan, *Entomobrya*, in the litter layer. We detected no cascading effects from the natural density of *M. yunnanica*, and changes in spider densities had no cascading effects on microbial biomass. Modifying spider densities can generate a trophic cascade effect and alter leaf litter decomposition, with a potential to influence ecosystem function in tropical forest floors. This study suggests that trophic interactions in detritus-based food webs should be considered to better understand soil organic matter dynamics in tropical forests.

1. Introduction

Trophic cascades, the indirect effects of predators on non-adjacent trophic levels, have long been recognized in the ecological literature [1–4]. In terrestrial arthropod-dominated food webs, predator removal led to increased densities of herbivorous insects and higher levels of plant damage [5–7]. Top-down effects of predators could cascade into plant diversity and hence alter the quality and quantity of plant material decomposed prior to entering the soil organic matter pool [8,9]. Cascading effects of predators have been examined most often in food webs based on living plant matter [7,10]. In contrast, the role of predators in detritus-based food webs has been less explored [11]. Additionally, approximately 70–90% of terrestrial primary production enters detrital food webs [12], so trophic interactions in detritus-based food webs could have great potential to influence ecosystem functioning such as litter decomposition and nutrient release [13,14].

Trophic cascade effects of predators are generally considered to be weaker in detrital than in living food webs [15–18]. This is because the detrital food webs are characterized by high species diversity, long food chains, and high spatial and temporal heterogeneity [19,20]. Hence, terrestrial detrital food webs possess multiple features that are predicted to attenuate top-down effects of predators [21–23]. Nonetheless, theoretical and accumulating empirical evidence both suggest that predators can have cascading effects on forest-floor food webs and ecosystem processes by depressing densities and species composition of soil fauna, thereby indirectly affecting ecological process, such as rates of decomposition [11,24–27]. However, no general patterns of cascading effects have been identified in these settings. For example, Lawrence and Wise [24] found that reducing spider densities could increase rates of decomposition, accompanied by increased in collembolan densities in a deciduous forest. However, a longer-term experiment found the opposite result in the same study site, with litter decomposing more rapidly at higher spider densities [25]. In addition, Miyashita and Niwa [26] showed that decreasing spider abundance increases collembolan density, but it did not change litter decomposition rates. This discrepancy among these different studies highlights the complexity of forest-floor food webs [28].

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Additionally, most previous studies have focused on the interactions between wandering spiders and collembolans, but the potential prey of ground-dwelling spiders consists of Diptera larvae, Coleoptera and, to a lesser extent, Hemiptera in addition to collembolans [29]. Few studies have investigated the effect of web-building spider predation on the soil fauna community in tropical forests.

Spiders represent a large fraction of arthropod predator biomass in forests and meadows [30–32] and they exhibit substantial temporal and spatial variability in terms of species abundance and diversity [28]. Previous studies at the habitat scale showed that forest floor spider density and diversity are correlated with tree species identity, probably mediated by the quantity or quality of the litter layer [33–35]. Within-habitat distributions of litter-dwelling spiders also have high spatial and temporal heterogeneity, especially in highly heterogeneous tropical forests [36]. Spiders are sensitive to small-scale variations in abiotic conditions such as moisture, temperature and understory-vegetation density [37]. On the other hand, the prey availability may directly affect spider distribution, because predators can attain high abundances in the most rewarding patches [38,39]. The distribution of predators within heterogeneous habitats can have significant impacts on local prey populations with cascading effects on decomposition [40]. However, the relative importance of variation in predator abundance on prey composition and trophic cascade effects in forest floors is largely unknown [11].

In tropical forest floors, spiders are major predators with high diversity [41,42]. *Macrothele yunnanica* (*Macrothele*, Hexathelidae) is a dominant spider with regard to biomass and density in the tropical forest floor of Xishuangbanna, southwest China [43]. *M. yunnanica* is a sit-and-wait predator that has a continuous presence within a fixed habitat location, and thus may provide a persistent point-source cue of high risk to prey [9]. The presence of *M. yunnanica* may influence the activity and density of prey species. In this study, we manipulated densities of this dominant web-building spider *M. yunnanica* in a tropical rainforest floor, and asked what are: (1) the direct effects of *M. yunnanica* density on soil fauna in tropical forest floor; (2) the potential trophic cascade effects of *M. yunnanica* on rate of leaf litter decomposition; (3) the further trophic cascade effects of *M. yunnanica* on microbial biomass carbon and nitrogen.

2. Materials and methods

2.1. Study site and the spider

This study was conducted in a tropical secondary forest (21° 55′ N, 101° 12′ E, 580 a.s.l.) at the Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences (CAS), Xishuangbanna, Yunnan, southwest China. This region has a tropical monsoon climate. Mean annual air temperature is 21.5 °C, ranging from 14.8 °C in the coldest month (January) to 25.5 °C in the hottest month (June), with zero days of frost. The mean annual wind speed is 0.5 m s^{-1}. Annual precipitation averages 1557 mm, of which 85% occurs during the May to October rainy season. The soil type in the study site is Oxisol. The annual litter fall is 122.3 ± 7.9 g m^{-2} (mean ± SE) and the C/N ratio of leaf litter is 28.9 ± 2.3 (mean ± SE). Yet due to the high rate of decomposition in this tropical area, the average depth of litter layer is only 1.0 cm [44]. The tropical secondary forest is dominated by 30–50 year old successional trees that naturally recolonized the area after it was no longer used for agriculture. The 20–25 m canopy is composed mainly of *Gnetum montanum*, *Litsea glutinouse*, *Castanopsis indica*, *Phoebe lanceolata*, and *Schefflera venulosa*.

Macrothele yunnanica can live for about two years and is a dominant spider with regard to biomass and density in this study site [43,45]. *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 ground. *M. yunnanica* stay in their silk-lined tubular burrow retreats. When potential prey contacts the trip-lines, the spider rushes out and subdues it by venom injection.

2.2. Experimental design

In early September 2011, we established thirty plots (1 × 1 m) with 60-cm high external fences in the tropical secondary forest and randomly assigned these plots to one of 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 and this density is similar with its mean density in this study site; **Ten spiders:** where 10 adult *M. yunnanica* spiders were kept in the plots. The reason for the latter treatment is that *M. yunnanica* exhibit obvious temporal and spatial variation in species abundance, and *M. yunnanica* aren't randomly distributed and they can attain high abundances in small patches (about 10 individuals per 1 m^2, S. Liu *personal communication*). All plots were located in relatively flat area and the distance between plots was about 5 m. 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 limit migration of spiders. We transferred leaf litter accumulated on these screens back into the plots.

After fencing the plots, large spiders and other common predators, such as carabid beetles, Opiliones, chilopodes, were first removed by hand from plots, and then we carefully sifted all of the litter in each plot through a 5-mm mesh screen *in situ*, removing all spiders and other predators encountered in these plots. All other soil fauna were returned to plots. Two weeks later, we released 6 and 10 adult *M. yunnanica* individuals in **Six spiders** and **Ten spiders** plots, respectively. Spiders were collected locally from our study site. Spider abundance was manipulated two or three times per month and this experiment continued for one year. After the start of experiment, we checked and replenished *M. yunnanica* at the relevant treatments, and we did not sift litter again. We note that Lawrence and Wise [25] demonstrated that neither sifting litter nor fencing plots influenced rates of leaf litter disappearance.

To evaluate rate of litter disappearance, we employed the litter bag technique [46]. We selected 2-mm and 1-mm nylon mesh bags (20 × 20 cm) according to the body size (width) of litter fauna [46]. It is expected that most macro, meso, and microfauna can enter the 2-mm bags, thus we treat them as our control. Only meso and microfauna may invade the 1-mm mesh bags, thus excluding most macrofauna. Five bags for each mesh size (ten bags total) were set below the current-year litter and attached to the ground in each plot. To reduce the risk of impacting the activity of spiders, we added the litter bags before releasing *M. yunnanica* individuals. We selected single-species *G. montanum* (leaf litter C:$N = 16.6$), a dominant plant species in our study site, as an indicator of the potential of spiders to influence litter decomposition. *G. montanum* leaf litter was collected locally from our study site and left to air dried for two weeks before use. Ten grams of dry *G. montanum* leaf litter was placed in each bag. A subsample of extra 30 bags (15 litter bags per mesh size from each plot) was collected and returned to the laboratory immediately after placement in the plot. These bags were oven-dried at 60 °C until they reached a constant weight so that dry mass lost due to handing could be determined [47].