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Net neutral effects of a generalist vertebrate predator on seed production result from simultaneous suppression of plant antagonists and mutualists

Jiyan Zhao[a], Kai He[b], Youheng Peng[c], Xinwei Wu[a,*], Shucun Sun[a,c]

[a] *Department of Biology, Nanjing University, Nanjing 210093, China*
[b] *College of Materials and Chemistry & Chemical Engineering, Chengdu University of Technology, Chengdu 610059, China*
[c] *Center of Ecological Studies, Chengdu Institute of Biology, Chinese Academy of Sciences, Chengdu 610041, China*

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Abstract

Trophic cascade theory predicts that predators may confer a positive effect on plants through suppressing plant antagonists or a negative effect through limiting plant mutualists, but these positive and negative cascading predator effects have seldom been examined in combination. In a marshy Tibetan alpine meadow, we conducted a factorial experiment (presence vs. absence of both predators and herbivores) using replicate field enclosures over a growing season to determine the effects of the generalist predator, the plateau frog (*Rana kukunoris*), on the density of herbivorous grasshoppers (*Chorthippus fallax*) and the visitation rate of insect mutualists (pollinators), as well as corresponding levels of leaf damage and seed production in a Tibetan lotus (*Saussurea nigrescens*). Frogs reduced the capitulum visitation rate of insect pollinators. Frogs also reduced grasshopper density and the corresponding leaf damage in the plants. Consequently, simultaneous suppression of plant antagonists and mutualists resulted in net neutral effects of frogs on seed set ratio and seed number per capitulum in *S. nigrescens*. Our study suggests that simultaneously examining the effects of predators on plant mutualists and antagonists is necessary to fully understand the roles of generalist predators in natural food webs.

Zusammenfassung

Die Theorie der trophischen Kaskaden sagt voraus, dass Prädatoren einen positiven Effekt auf Pflanzen ausüben können, indem sie Antagonisten unterdrücken, oder einen negativen, indem sie Mutualisten unterdrücken, aber diese positiven und negativen Räubereffekte sind selten gemeinsam untersucht worden. Auf einer alpinen tibetanischen Feuchtwiese führten wir ein voll faktorielles Experiment durch (mit An- und Abwesenheit von Räubern und Herbivoren). Wir nutzten replizierte Käfige im Freiland während der Vegetationsperiode, um den Einfluss des generalistischen Plateaubraunfrosches (*Rana kukunoris*) auf die Dichte von pflanzenfressenden Heuschrecken (*Chorthippus fallax*) und die Besuchszahlen von mutualistischen Insekten (Bestäuber) sowie auf die entsprechenden Raten von Blattfrass und Samenproduktion bei einer tibetanischen Alpenscharte

*Corresponding author. Tel.: +86 025 83686670; fax: +86 025 83686670.
E-mail address: wuxw@nju.edu.cn (X. Wu).

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(*Saussurea nigrescens*) zu untersuchen. Die Frösche reduzierten den Blütenbesuch der Insekten. Sie reduzierten ebenfalls die Dichte der Heuschrecken und die Blattschäden. In der Konsequenz resultierte aus der gleichzeitigen Verringerung von Antagonisten und Mutualisten ein neutraler Nettoeffekt der Frösche auf den relativen Samenansatz und die Samenanzahl je Körbchen bei der Alpenscharte. Unsere Studie legt nahe, dass die gleichzeitige Untersuchung der Einflüsse eines Räubers auf Mutualisten und Antagonisten der Pflanze notwendig ist, um ein vollständiges Verständnis der Rolle von generalistischen Räubern in natürlichen Nahrungsnetzen zu erreichen.

Keywords: Density-mediated indirect interactions; Herbivore; Pollinator; Tibetan Plateau; Top-down control; Trophic cascade

Introduction

Predators can modify community structure and ecosystem functioning by generating trophic cascading effects (Hairston, Smith, & Slobodkin 1960; Paine 2002; Schmitz 2008; Griffin et al. 2011; Karp & Daily 2014) that operate through a wide variety of pathways (Pearson 2010). These different types of interactions are usually measured in separate studies, and often in separate ecosystems. Particularly, much attention has been focused on predator effects in predator-herbivore-plant interactions, showing that predators can reduce leaf damage, facilitate plant growth, and enhance plant fitness (e.g. Vasconcelos 1991; Schmitz, Hambäck, & Beckerman 2000; Dawes-Gromadzki 2002; Romero & Koricheva 2011). In contrast, predators have been also illustrated to confer negative effects on plant reproduction by suppressing plant mutualists in predator-pollinator-plant interactions (Suttle 2003; Muñoz & Arroyo 2004; Dukas 2005; Meehan, Lease, & Wolf 2005; Wang, Geng, Ma, Cook, & Wang 2014). Accordingly, net results of cascading predator effects on plants depend on whether the predator suppresses plant antagonists or mutualists.

Most predator species are generalists with a broad diet spectrum (Scheu 2001), and some of them simultaneously interact with both plant antagonists and mutualists (Knight, Chase, Hillebrand, & Holt 2006). In particular, a single predator species may simultaneously suppress both herbivores and pollinators. For example, crab spiders can capture various flower visiting insects, including flower herbivores such as beetles and moths, as well as pollinators such as honeybees and even bumblebees (Dukas & Morse 2003; Suttle 2003; Dukas 2005; Robertson & Maguire 2005; Ings & Chittka 2009), and many birds and reptiles known as predators of phytophagous insects also consume insect pollinators (Suttle 2003; Muñoz & Arroyo 2004; Meehan et al. 2005). These examples imply that a single generalist predator species may have contrasting effects on plant fitness (Romero & Koricheva 2011).

Indeed, a single predator can have contrasting effects on plants through directly suppressing plant antagonists or mutualists, and signs of the net effects can be negative, positive or neutral, depending on the relative influence of the predator on the interaction pathways (Knight et al. 2006). To the best of our knowledge, there are only four studies explicitly showing such a dual role of predators on plants. In a modeling study, Higginson, Ruxton, and Skelhorn (2010) showed that flower-dwelling predators would have net positive effects on the plant if both the pollinators and the granivores were at high densities. In a field investigation, Romero, Souza and Vasconcellos-Neto (2008) found that the South American lynx spiders (*Peucetia flava* and *P. rubrolineata*) had overall positive effects on the fitness of a neotropical glandular shrub (*Trichogoniopsis adenantha*). The spiders significantly reduced the damage to the leaves, capitula, ovaries, corollas, and stigmas by efficiently consuming several species and guilds of herbivores on the leaves and inflorescences, whereas their negative influence on ovary fertilization was non-significant despite low abundance of flower visitors in the presence of predators. Similar effects were also found in the flower-dwelling spider species *Misumenops argenteus* (Romero & Vasconcellos-Netor 2004). More recently, Ohm and Miller (2014) revealed that several ant species (*Crematogaster opuntiae* and *Liometopum apiculatum*) reduced pollinator visitation and seed production in the cholla cactus *Opuntia imbricate*, and this negative effect on plants could be balanced by the benefits of long-term protection from herbivores provided by the ants. Nevertheless, these studies focus exclusively on invertebrate predators, and the empirical evidence for the dual functional role of predators on plant fitness is still sparse for single predator species, and completely lacking for terrestrial vertebrate predators.

Frogs are well known as generalist predators in many ecosystems, and their diets include herbivores, pollinators and detritivores (Freed 1980; Beard, Eschtruth, Vogtt, Vogtt, & Scatenat 2003; Wu, Zhang, Griffin, & Sun 2014). In Tibetan alpine meadows, the adults of the frog species *Rana kukunoris* are widespread (Wu et al. 2014) and are known to feed upon phytophagous insects such as grasshoppers, potentially reducing proportional leaf damage and enhancing plant reproduction in the meadows. Meanwhile, this generalist insectivore may also prey on small pollinators such as flies and honeybees, which are primary flower visitors of plants with large corollae such as Tibetan lotus *Saussurea nigrescens* (Mu et al. 2014). We hypothesize that *R. kukunoris* will confer an indirect negative effect on seed production in *S. nigrescens* via the plant-pollinator-predator