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The brown-world role of insectivores: Frogs reduce plant growth by suppressing detritivores in an alpine meadow

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Abstract

Predators of plant-suppressing herbivores have long been known to indirectly enhance plant biomass, while more recent work has revealed that predators of plant-facilitating detritivores can have the opposite effect on plant biomass. Generalist predators, such as frogs that typically facilitate plant growth in green food webs, may potentially negatively affect plant growth by consuming prey from brown food webs. In a marshy Tibetan alpine meadow, we tested the hypothesis that the locally abundant frog *Rana kukunoris* could negatively affect plant growth through suppression of dung-decomposing detritivores that promote plant growth by enhancing nutrient recycling. We conducted a factorial experiment (presence/absence of predators × presence/absence of dung) using replicate field enclosures over a growing season. Where dung was present, frogs significantly reduced the number of dung-feeding beetles and dung-feeding flies (including fly eggs and maggots) per dung pat, thereby decreasing dung mass loss and, indirectly, aboveground plant biomass (by 22%) surrounding dung pats. Where dung was absent, frogs did not affect plant biomass. Moreover, the number of dung beetles was positively associated with dung mass loss and soil soluble *N* concentration (but not total *N* concentrations), which in turn positively correlated with aboveground plant biomass. These results indicate that a generalist predator species standing in green food webs may play a contrasting role in brown food webs and indicate that a more nuanced appreciation of the functional role of predators in tri-trophic systems is required to accurately predict their cascading effects. Future studies must assess the relative strength of cascading effects mediated through brown and green channels in order to assess the net cascading effects of generalist predators in natural food webs.

Zusammenfassung

Es ist seit langem bekannt, dass die Räuber von Pflanzen kontrollierenden Herbivoren indirekt die Pflanzenbiomasse steigern, während neuere Untersuchungen aufdeckten, dass Räuber von Pflanzen fördernden Detrivoren den entgegengesetzten Effekt auf die Pflanzenbiomasse haben können. Generalistische Räuber, wie z.B. Frösche, die typischerweise das Pflanzenwachstum in grünen Nahrungsnetzen befördern, könnten das Pflanzenwachstum negativ beeinflussen, indem sie Beutetiere aus den braunen Nahrungsnetzen konsumieren. Auf einer alpinen Feuchtwiese in Tibet testeten wir die Hypothese, dass die lokal häufige Froschart *Rana kukunoris* das Pflanzenwachstum negativ beeinflussen könnte, und zwar durch die Reduktion von Dungfressern, die das Pflanzenwachstum durch die Verstärkung des Nährstoffumsatzes fördern. Wir führten über eine Vegetationsperiode hinweg ein faktorielles Freilandexperiment (mit/ohne Räuber × mit/ohne

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Dung) mit replizierten Käfigen durch. Wo Dung vorhanden war, reduzierten die Frösche signifikant die Abundanz der dungfressenden Käfer und Fliegen (einschließlich der Fliegeneier und Maden), wodurch der Gewichtsverlust der Fladen und, indirekt, die oberirdische Pflanzenmasse in der Umgebung der Fladen (um 22%) reduziert wurden. In Behandlungen ohne Dung beeinflussten die Frösche die pflanzliche Biomasse nicht. Die Anzahl der Dungkäfer war positiv mit dem Gewichtsverlust des Dungs und der Konzentration löslichen Stickstoffs im Boden verbunden (nicht aber mit der Gesamt-Stickstoffkonzentration), welche ihrerseits positiv mit der oberirdischen Pflanzenbiomasse korreliert waren. Diese Ergebnisse zeigen, dass eine generalistische Räuberart, die in einem grünen Nahrungsnetz fußt, eine entgegengesetzte Rolle in einem braunen Nahrungsnetz spielen kann, und sie zeigen, dass eine differenziertere Einschätzung der funktionellen Rolle von Räubern in tritrophischen Systemen erforderlich ist, um ihre kaskadierenden Effekte genau vorherzusagen. Zukünftige Studien müssen die relative Stärke der Kaskadeneffekte, die über grüne und braune Kanäle vermittelt werden, erfassen, um die Netto-Kaskadeneffekte abzuschätzen, die von generalistischen Räubern in natürlichen Nahrungsnetzen bewirkt werden.

Keywords: Density-mediated indirect interactions; Detritus food webs; Ecosystem functioning; Tibetan Plateau; Top-down control; Trophic cascade

Introduction

Predators play important ecological roles in community assembly and ecosystem functioning (Hairston, Smith, & Slobodkin, 1960; Paine, 2002; Duffy, Richardson, & France, 2005; Schmitz, 2008; Griffin et al., 2011). Classic food web theories based on the predator-herbivore-plant (P-H-P) pathway (Hairston et al. 1960) highlight that predators can indirectly facilitate primary productivity in autogenic ecosystems via a top-down trophic cascade (a so-called 'green world' role of predators). Numerous case studies have validated this idea in aquatic systems (Duffy et al. 2005), grasslands (Schmitz, 2008), intertidal rocky shores (Paine, 2002) and salt marshes (Silliman & Bertness, 2002). More recently, empirical examples have broadened our appreciation of cascading effects of predators by revealing how they can indirectly suppress primary productivity in grassland ecosystems by suppressing intermediate detritus-consumers in a predator-detritivore-plant (P-D-P) pathway (a so-called 'brown world' role of predators; Moore, McCann, Setala, & De Ruiter, 2003; Wu, Duffy, Reich, & Sun, 2011). Consequently, generalist predators, which typically stand in P-H-P chains, may influence plant growth via a P-D-P pathway by consuming prey from detritus food webs (Scheu, 2001).

The dual functional roles of single predators in P-H-P and P-D-P interaction chains may be common in nature (Scheu, 2001). Indeed, species that are considered to be important regulators of herbivores also appear to widely interact with detritivores: for example, aboveground spiders and ground beetles can prey upon major detritivores (Wise, Snyder, Tuntibunpakul, & Halaj, 1999; Halaj & Wise, 2002; Miyashita & Takada, 2007); predatory birds and woodland salamander may consume earthworms and other soil micro-invertebrates (Csermely & Bagni, 2003; Ransom, 2012); and aboveground predatory amphibians efficiently eat litter-feeders (Sin, Beard, & Pitt, 2008). These examples illustrate that species presumed to have an entirely positive indirect effect on plants via the P-H-P pathway may also influence plants negatively via the P-D-P pathway. Despite this widespread potential, empirical tests of the cascading effects of generalist insectivores through the P-D-P pathway are still largely lacking (but see Kajak, 1997; Lawrence & Wise, 2000).

Frogs are widely known to suppress herbivorous insects and thereby increase plant growth and crop yield in natural and managed ecosystems (Beard, Eschtruth, Vogtt, Vogtt, & Scatenat, 2003; Xu, Fujiyama, & Xu, 2012). For instance, in the Luquillo Experimental Forest in the north-eastern corner of Puerto Rico a terrestrial frog species *Eleutherodactylus coqui*, increased foliage production rates by 80% via reducing aerial invertebrates and leaf herbivores (Beard et al. 2003). In Tibetan alpine meadows, the adults of a frog species (*Rana kukunoris*) is widespread (particularly in low-lying wet areas) and are known to feed upon herbivores, potentially enhancing plant growth in the meadows. However, this species is a generalist insectivore, also known to prey heavily on detritivores such as dung beetles and flies (Zhang, Li, Dai, & Wang, 2010), both of which can facilitate plant growth by enhancing dung removal rate and soil nutrient availability (see review by Nichols et al. 2008; Wu & Sun, 2010). We therefore hypothesized that *R. kukunoris* may have an indirect negative effect on plant biomass via the P-D-P pathway. We tested this hypothesis by conducting a factorial experiment (presence/absence of predators × presence/absence of dung), examining the effects of frogs on the detritivores, dung removal rates, soil properties, and aboveground plant biomass. We predicted that the predatory frogs would directly decrease the abundance of the detritivores and dung removal rate, and then indirectly reduce soil nutrient availability and plant growth.

Materials and methods

Study site and natural history

This study was conducted in the Alpine Meadow Research Station (32°48′ N, 102°33′ E), Hongyuan Country, Sichuan province, eastern Qinghai-Tibetan Plateau. The altitude is