



No detectable trophic cascade in a high-Arctic arthropod food web



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Abstract

In so-called trophic cascades, a predator may influence the non-adjacent trophic level by suppressing the abundance and/or altering the traits of its prey. In the Arctic, the occurrence of trophic cascades seems particularly likely due to the restricted number of interacting species. Spiders are abundant, and their predation of herbivorous insects has been recognized as a potentially important structuring force of the community. To test whether variation in spider abundance results in trophic cascades through an arctic food chain, we explored how the abundance of the wolf spider *Pardosa glacialis* is reflected in herbivore damage on the plants of a high-Arctic locality: the Zackenberg Valley in Northeast Greenland. We first established observational transects to reveal that local variation in spider densities is indeed reflected in local variation in caterpillar herbivory on mountain avens (*Dryas octopetala x integrifolia*) and arctic willow (*Salix arctica*). We then used two types of enclosures to manipulate local densities of *P. glacialis* and/or of the herbivore *Sympistis nigrita*. While these treatments were successful in altering predator and herbivore densities, the manipulation of spider densities had no detectable effect on levels of plant damage or seed production. The results indicate that spiders as predators are unable to suppress the herbivores in Northeast Greenland. While surprising, this lack of cascading effects might be attributable to the general diet of wolf spiders. *P. glacialis* may feed on the predator, the herbivore, the decomposer and/or the pollinator guilds of the food web, thereby diluting the predation pressure in multiple directions. Thus, the terrestrial food webs of the Arctic seem both complex and robust against cascading effects from fluctuations in the densities of single species.

Zusammenfassung

In sogenannten trophischen Kaskaden kann ein Räuber eine nicht angrenzende trophische Ebene beeinflussen, indem er die Abundanz seiner Beute verringert und/oder die Eigenschaften seiner Beute verändert. In der Arktis erscheint das Auftreten von trophischen Kaskaden aufgrund der begrenzten Anzahl interagierender Arten besonders wahrscheinlich. Spinnen sind abundant, und ihr Räuberdruck auf die Herbivoren wurde als eine potentiell wichtige strukturierende Kraft in der Gemeinschaft erkannt. Um zu testen, ob eine Veränderung der Spinnenabundanz trophische Kaskaden in einer arktischen Nahrungskette auslöst, untersuchten wir, wie die Abundanz der Wolfsspinne *Pardosa glacialis* sich in den Fraßschäden an den Pflanzen in

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einem Gebiet der Hocharktis, dem Zackenbergtal in Nordost-Grönland abbildet. Wir richteten zuerst Beobachtungstransekte ein, um festzustellen, dass sich die lokale Variation der Spinnendichten tatsächlich in der lokalen Variation des Raupenfraßes an der Silberwurz (*Dryas octopetala x integrifolia*) und der Arktischen Weide (*Salix arctica*) widerspiegelt. Wir richteten dann zwei Typen von Käfigen ein, um die Abundanzen von *P. glacialis* und/oder des Herbivoren *Sympistis nigrita* (Noctuidae) zu manipulieren. Während diese Behandlungen die Räuber- und Herbivorendichten erfolgreich veränderten, hatte die Manipulation der Spinnendichten keinen erkennbaren Effekt auf den Grad des Fraßschadens oder die Samenproduktion. Die Ergebnisse zeigen an, dass Spinnen als Prädatoren nicht in der Lage sind, die Herbivoren in Nordost-Grönland zu kontrollieren. Dieses Fehlen eines Kaskadeneffekts könnte auf das generalistische Nahrungsspektrum der Wolfsspinnen zurückzuführen sein. *P. glacialis* könnte Beutetiere aus den Räuber-, Herbivoren-, Zersetzer- und/oder Bestäuber-Gilden des Nahrungsnetzes fangen, wodurch der Räuberdruck in mehrere Richtungen gemindert wird. Damit scheinen die terrestrischen Nahrungsnetze der Arktis sowohl komplex als auch robust gegen Kaskadeneffekte, die sich aus Populationsschwankungen einzelner Arten ergeben könnten, zu sein.

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Introduction

Predators are important in shaping the structure of food webs. Beyond their direct influence on prey populations, predators can also indirectly affect other species within the same food web through phenomena like trophic cascades (Sih, Crowley, McPeek, Petranka, & Strohmeier, 1985; Schmitz, Hambäck, & Beckerman, 2000). In a trophic cascade, the predator indirectly influences the food source of its prey. The predator may either change the abundance of its prey by direct predation or by altering the behavior of the prey species by so-called trait-mediated indirect interactions (Cronin, Haynes, & Dillemuth, 2004; Schmitz, Beckerman, & O'Brien, 1997). Both types of indirect effects have been recognized in various ecosystems and identified as important factors shaping food webs and communities (Estes et al., 2011; Hairston, Smith, & Slobodkin, 1960; Oksanen, Fretwell, Arruda, & Niemelä, 1981; Schmitz et al., 2000; Terborgh & Estes 2010). So far, most research on trophic cascades has focused on the effects of predators on herbivory, but other interactions might be affected as well (Knight, Chase, Hillebrand, & Holt, 2006). Predators may prey on plant mutualists, like pollinators, resulting in negative indirect effects on the plant. Such effects seem both common and strong in different food webs (Knight et al., 2006).

Arctic food webs offer ideal settings for studies of trophic cascades. A general decrease in species diversity with increasing latitude (Allen, Brown, & Gillooly, 2002; Lewinsohn & Roslin, 2008; Wright, 1983) results in arctic food webs having relatively few interacting species (Oksanen & Oksanen, 2000). This facilitates the recognition and measurement of indirect effects and makes the occurrence of trophic cascades likely.

A defining feature of terrestrial arctic invertebrate communities is the scarcity of ants and beetles, both major groups of insect predators at lower latitudes (Born &

Böcher, 1998; Jeanne, 1979; Wirta, Weingartner, Hambäck, & Roslin, 2015). Instead, spiders are abundant and have been hypothesized to act as the dominant arthropod predators in many parts of the Arctic (Larsen, 2000; Roslin, Wirta, Hopkins, Hardwick, & Várkonyi, 2013). Spiders preying on insects can indirectly affect plants in two opposing ways (Knight et al., 2006). First, by reducing the number of herbivores or by scaring them away, a high predation pressure exerted by spiders may enhance the growth and survival of plants. Second, and in contrast to the first alternative, spiders may disturb seed production of plants, by preying on their pollinators. Thus spiders could exert both beneficial and detrimental indirect effects on plants. To examine both alternatives, we studied the role of invertebrate predators in a high-Arctic arthropod community by complementary observational and experimental methods.

Given the high abundance of the predatory wolf spider *Pardosa glacialis* (Larsen, 2000; Wirta et al., 2015), we specifically focused on the effects of this species on plants. To detect effects of spiders on herbivory, we measured herbivore damage on two of the main plant species in the study area, mountain avens (*Dryas octopetala x integrifolia*; see Bay, 1998) and arctic willow (*Salix arctica*). To detect possible effects of predation on pollination, we recorded the occurrence of seed heads of mountain avens. In particular, we expected high densities of wolf spiders to depress the herbivore and/or pollinator populations, and to thus result in low levels of plant damage and/or impaired levels of seed sets. This expectation of trophic cascades derived from the features of the study system (see below and Appendix A), as preliminarily suggesting a simple, chain-like food web.

Materials and methods

Study system and species

This study was carried out at Zackenberg Research station, located in the Zackenberg valley of Northeast Greenland

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