GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 12 (2011) 523–531

Basic and Applied Ecology

www.elsevier.de/baae

# Bottom-up trophic cascades caused by moose browsing on a natural enemy of a galling insect on balsam fir

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Received 3 February 2011; accepted 23 June 2011

## Abstract

To elucidate the impact of browsing by moose on the indigenous insect community, we investigated the abundance of a specialist insect herbivore (galler; *Paradiplosis tumifex*) and its natural enemy (inquiline; *Dasineura balsamicola*) on balsam fir saplings in the field using exclosures in Newfoundland, Canada. The number of current-year shoots on each sapling, but not the density of balsam fir saplings, was significantly higher inside exclosures, where moose had been excluded for 9–12 years, than outside exclosures. Current-year shoots were longer and contained more, but smaller, needles inside than outside exclosures. Moose browsing had a negative impact on the abundance of both the galler and its natural enemy. Gall density was 85.6% and 60.4% lower in 2006 and 2007, respectively, outside than inside exclosures. Similarly, the attack rate of *D. balsamicola* was 76.5% lower outside than inside exclosures in 2007. The apparent survival rate of *P. tumifex* larvae was similar outside and inside exclosures due to higher rates of unexplained mortality in galls outside exclosures. Survival of *P. tumifex* larvae was positively related to shoot length and inversely related to gall density. Only gall density was negatively related to *D. balsamicola* survival. Our results demonstrate that a large mammal can cause strong bottom-up trophic cascades.

## Zusammenfassung

Um den Einfluss der Beweidung durch Elche auf die indigene Insektengemeinschaft aufzuklären, untersuchten wir die Abundanz eines spezialisierten Herbivoren, des Gallbildners *Paradiplosis tumifex*, und seines Antagonisten, des Inquilins *Dasineura balsamicola*, auf jungen Balsamtannen im Freiland und nutzten dafür Ausschlussflächen auf Neufundland, Kanada. Die Anzahl der diesjährigen Triebe auf jedem Jungbaum, aber nicht die Dichte der Jungbäume, war innerhalb der Einzäunungen, von denen Elche neun bis zwölf Jahre ausgeschlossen waren, signifikant höher als außerhalb. Die diesjährigen Triebe waren auf den Ausschlussflächen länger und besaßen mehr, aber kleinere Nadeln als außerhalb. Die Beweidung durch Elche hatte einen negativen Einfluss auf den Gallbildner und den Inquilin. Die Gallendichte war außerhalb 85,6% (2006) bzw. 60.4% (2007)

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doi:10.1016/j.baae.2011.06.007

geringer als innerhalb der Einzäunungen. Der Befall durch *D. balsamicola* war 2007 außerhalb 76,5% geringer als innerhalb. Die apparente Überlebensrate der *P. tumifex*-Larven war aber innerhalb und außerhalb der Ausschlussflächen ähnlich groß, was auf höhere Raten ungeklärter Mortalität außerhalb der Einzäunungen zurückzuführen ist. Das Überleben von *P. tumifex* war positiv mit der Trieblänge korreliert und negativ mit der Gallendichte. Die Überlebensrate von *D. balsamicola* war allein und negativ mit der Gallendichte korreliert. Unsere Ergebnisse zeigen, dass ein Großsäuger starke trophische bottom-up Kaskaden verursachen kann.


***Keywords:*** Cascading effects; Gall midge; Indirect interaction; Inquiline; Ungulate herbivory

## Introduction

Mammal browsing can cause important changes in food-web structures of terrestrial ecosystems (reviewed by Côte, Rooney, Tremblay, Dussault, & Waller 2004; Suominen & Danell 2006; Larson & Paine 2007). High levels of browsing by mammals may cause bottom-up trophic cascades on insect communities by reducing the density or size of host plants available to phytophagous insects and by fragmenting their distribution. Previous studies evaluating the effects of mammal browsing on insect communities have focused primarily on the abundance of insect herbivores (reviewed by Stewart 2001; Suominen & Danell 2006) and less on their natural enemies (but see Ueda, Hino, & Tabuchi 2006; Vanbergen, Hails, Watt, & Jones 2006). Understanding not only the abundance, but also the mortality factors and reproductive performance of insect herbivores (e.g., Tabuchi, Ueda, & Ozaki 2010) will enable better predictions of the long term impacts of mammal browsing. Natural enemies are a major mortality factor for insect herbivores (Bailey & Whitham 2003; Ueda et al. 2006), and the degree and mechanisms by which they are influenced by browsing may differ from those influencing insect herbivores. However, empirical study of bottom-up trophic cascades caused by mammal browsing in the field is limited. Explaining the processes of such bottom-up trophic cascades caused by mammal browsing is essential for predicting changes in biodiversity and for conserving ecosystems.

On the island of Newfoundland, Canada, vegetation has been simplified by repeated and intensive browsing by moose (*Alces alces* L.) that were introduced in 1904 (Thompson, Curran, Hancock, & Butler 1992; Thompson & Curran 1993; McLaren, Mahoney, Porter, & Oosenbrug 2000). Browsing by moose has removed most hardwoods from many areas (Bergerud & Manuel 1968) and the major component of forests has changed from balsam fir *Abies balsamea* (L.) Mill (Pinaceae) to black spruce *Picea mariana* (Mill.) B.S.P. (Pinaceae) (Thompson et al. 1992; Thompson & Curran 1993). Moose browsing may have influenced the quality as well as the quantity of balsam fir available for insect herbivores because saplings that have survived repeated browsing by moose are much shorter and thinner than unbrowsed trees. Such degraded host plants may cause strong cascading effects, such as severe decline of natural enemies of insect herbivores that are prone to being disturbed (Tscharntke & Brandl 2004) by the population fluctuations of insect herbivores.

To evaluate the potentially cascading effects of moose browsing on the insect community on balsam fir, we investigated the abundance of balsam gall midge *Paradiplosis tumifex* Gagné (Diptera: Cecidomyiidae), which is a specialist insect herbivore of balsam fir, and its antagonistic inquiline *Dasineura balsamicola* (Lintner) (Diptera: Cecidomyiidae) in the field using exclosures. The specific objective of this study was to determine whether the abundance and potential fecundity (i.e., larval weight) of both insect herbivore and its natural enemy are affected by trait-mediated changes of balsam fir saplings due to moose browsing. We compared the density of balsam fir trees and number of current-year shoots, which are attacked by *P. tumifex*, to the density of galls per shoot, survival of *P. tumifex* larvae, and the rate of inquilinism inside and outside of exclosures. Similarly, we evaluated the influence of browsing on needle density and size and on larval weight which is related to potential fecundity in another midge species (Tscharntke 1988). We examined how mammal browsing causes cascading effects on a natural enemy through changes of abundance or quality of organisms at lower trophic positions (i.e., an insect herbivore and its host plant). In this study, we predicted that the abundance of both *P. tumifex* and *D. balsamicola* would negatively relate to moose browsing, and that larval weight of two insect species would negatively affected by decreased shoot length due to moose browsing, which relationship is predicted by plant vigor hypothesis (Price 1991) and optimal module hypothesis (Björkman 1998; McKinnon, Quiring, & Bauce 1998).

## Materials and methods

### Study organisms

*P. tumifex* is a common pest of balsam fir in North America (Osgood, Bradbury, & Drummond 1992). It is univoltine and mated females oviposit their eggs in bursting buds of balsam fir. Each larva induces one gall on a current-year needle. Galls become apparent in June, and enlarge in summer. Mature larvae drop to the ground in autumn to overwinter and pupate the following spring.