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Effects of insect herbivory on the performance of *Larix sibirica* in a forest-steppe ecotone

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Abstract

The potential of insects to cause temporary spatial shifts of the forest-steppe borderline was investigated in a case study in the northern Mongolian mountain taiga, where *Larix sibirica* forests border on montane meadow steppe. Insect herbivores of *L. sibirica* in northern Mongolia include gypsy moth (*Lymantria dispar*) and grasshoppers, which defoliate trees. Grasshoppers have (like mice) an additional detrimental effect by decorticating stems of tree seedlings. The hypothesis was tested that insect herbivores cause spatial shifts of the forest-steppe borderline by, first, increasing the mortality of mature trees and, secondly, inhibiting rejuvenation.

The first hypothesis was tested by investigating a *L. sibirica*-meadow steppe ecotone, which was heavily defoliated by gypsy moth in early summer 2005. Defoliation was more severe at the forest edge than in the forest interior. Though only 10% of the larch needles at the forest edge endured the gypsy moth invasion without feeding damage, trees were not sustainably affected, as trees were fully foliated in the subsequent year. This suggests that single gypsy moth invasions, which are frequent in Mongolia's forest-steppe ecotone, do not necessarily result in permanent damage of *L. sibirica* and, with it, not necessarily lead to local shifts of the treeline, though entire forest edges are often completely defoliated.

The second hypothesis was tested by planting 2-year-old seedlings of *L. sibirica* along the treeline towards the meadow steppe and in the interior of the adjacent light taiga forest. Seedling mortality within 3 months was significantly higher at the forest edge (87%) than in the forest interior (40%). Seedlings at the forest edge died either due to insect and small mammal herbivory (65%) or due to drought (25%). Herbivore damage in the seedlings included defoliation by gypsy moth and grasshoppers as well as decortication by grasshoppers and mice. The high feeding pressure for seedlings at the forest edge suggests that insects and mice inhibit or at least retard forest regeneration at the treeline and can thereby lead to temporary spatial shifts of the treeline towards the steppe, after trees have died, e.g., due to fire or logging.
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1. Introduction

Steppes in northern Mongolia and southern central Siberia primarily border on taiga forests of *L. sibirica* (Hilbig, 1995; Dulamsuren et al., 2005a). In Mongolia, *L. sibirica* covers 80% of the forested area (Gunin et al., 1999). Though modified by human activities (Hilbig et al., 2004; Rösch et al., 2005), the southern distribution limit of *L. sibirica* is generally controlled by drought (Gunin et al., 1999; Dulamsuren et al., in press). As water supply and evapotranspiration vary with the physiognomy of the landscape, the ecotone between forest and steppe is an aspect-dependent vegetation mosaic with forests on northern slopes and in dry valley and grasslands on southern slopes and in moist valley bottoms (Dulamsuren et al., 2005a,b).

Treelines towards the steppe are generally not static, but underlie spatial variation with temporarily varying influences of climate, fire activity, herbivore densities, and human utilization intensity (Jeffrey, 1961; Schwarz and Wein, 1999). Studies of temporal shifts of forest-steppe treelines include *L. sibirica* stands of northern Mongolia (Korotkov and Dorjsuren, 1988; Treter, 2000; Sankey et al., 2006).

Insect invasions are one possible cause that can lead to an expansion of grasslands into the forest. The highest potential to damage *L. sibirica* in northern Mongolia and southern Siberia among the insects has gypsy moth (*Lymantria dispar* L.). Gypsy moth in north-eastern Asia, where the species has evolved, is genetically distinct from western populations in Europe (Reineke and Zebitz, 1999). Asian populations have

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volant females and males and infest a wide range of tree species. European populations have a strong preference for oak and their females are incapable of flight. Gypsy moth was introduced to North America in the 19th or 20th century, respectively, from Europe and the Russian Far East (Liebhold et al., 1992; Régnière and Sharov, 1998). Outbreaks of gypsy moth in northern Mongolia and southern Siberia (Gninenko and Orlinskii, 2003) are more frequent and more persistent than in Europe. One reason for this is the dispersibility of the females. Furthermore, resistance to low winter temperatures and promotion by forest susceptibility to herbivore attacks (Williams et al., 1990; Sharov et al., 1999) probably contribute to the frequency of gypsy moth invasions in Mongolia and southern Siberia. High forest susceptibility can be assumed because trees occur in this area at their drought limit (Dulamsuren et al., in press; Li et al., 2007).

In Mongolia, gypsy moth often more or less completely defoliates entire forest edges towards the steppe (Fig. 1A). Forest edges are subject to more intense gypsy moth damage than trees in the forest interior, as gypsy moth females preferentially deposit their eggs on rock outcrops within the steppe (Fig. 1D) and gypsy moth larvae are wind-dispersed after hatching in springtime (Dulamsuren et al., in press). Though trees at forest edges infested by gypsy moth larvae are often so severely defoliated that they look dead, no information is available in the literature whether such damage in *L. sibirica* is reversible or not. Effects of feeding damage on tree vitality might be particularly severe in Mongolia, as *L. sibirica* regularly suffers from drought stress in addition (Dulamsuren et al., in press). In the present study, we therefore studied the effect of a severe gypsy moth outbreak in two consecutive years. The aim was to test the hypothesis that a massive gypsy moth invasion would result in the dieback of larch trees and, thus, in a local retreat of the treeline.

In addition to the impact of gypsy moth on mature trees, the potential of small herbivores at inhibiting the rejuvenation of *L. sibirica* was studied. Dulamsuren et al. (in press) showed with planting experiments that seedlings of *L. sibirica* in a northern Mongolian meadow steppe suffered from feeding by gypsy moth, grasshoppers and small mammals. In that study, feeding was more severe in the open meadow steppe than in the meadow steppe along the forest edge. This was attributed to the proximity to gypsy moth colonies and to the prevalence of polyphagous grasshoppers of the Oedipodinae, Calliptaminae, Decticinae and Bradyporinae in the open meadow steppe, whereas grass-eating grasshoppers of the Gomphocerinae were dominant at the forest edge (Dulamsuren et al., in press). In the present study, we

Fig. 1. (A) Edge of *Larix sibirica* forest bordering on montane meadow steppe in the forest-steppe belt of the Khangay, central Mongolia. Most trees are completed defoliated. (B–D) Study site in the Khentey, located in the northern Mongolian mountain taiga. (B) Defoliated larch after gypsy moth invasion in 2005. (C) Completely recovered trees at the same site in the year subsequent to the gypsy moth invasion (2006). (D) Colony of gypsy moth larvae in rock outcrop on the steppe slope bordering to the studied forest.

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