



Experimental habitat fragmentation and invertebrate grazing in a herbaceous grassland species

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Summary

A field experiment was conducted to examine the effects of habitat fragmentation on herbivore damage to individually tagged leaves of *Betonica officinalis* rosettes. Fragments of different size and corresponding control plots were established at three study sites in nutrient-poor calcareous grasslands in the northern Swiss Jura mountains. Leaf damage was recorded three times over the growing season (late spring, summer and early autumn). Five years after the initiation of the fragmentation, the density of rosettes did not differ between fragments and control plots. The number of leaves per rosette was higher in fragments than in control plots in summer but not in late spring and early autumn. The extent of leaf damage, expressed as proportion of leaf area removed by invertebrate herbivores, increased over the vegetation period. Leaf damage was greater in fragments than in control plots at two study sites, whereas the opposite (less strongly expressed) was found at the third site. Number of species and density (individuals per m²) of potential herbivores (gastropods and grasshoppers) were recorded in all fragments and control plots. Effects of fragmentation on the number of species and densities depended on plot size and differed between gastropods and grasshoppers. Leaf damage in fragments increased with increasing density of gastropods if the third site, which had lowest leaf damage, was excluded. Such a positive relationship was neither found in control plots nor for grasshopper densities. Thus, movement of gastropods in fragments was probably restricted which resulted in increased feeding pressure at least in two sites. However, even if our fragmentation experiment was well designed and replicated, the interpretation of these experimental results remains difficult because there was large site-to-site and seasonal variation.

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Zusammenfassung

Die Effekte der Habitatfragmentierung auf Frassschäden durch Herbivore an individuell markierten Blättern von *Betonica officinalis* Rosetten wurden in einem Feldexperiment untersucht. Dazu wurden unterschiedlich grosse Fragmente und entsprechende Kontrollflächen an drei verschiedenen Standorten mit Kalkmagerrasen im schweizerischen Jura etabliert. Die Frassschäden wurden dreimal während der Vegetationsperiode (Frühjahr, Sommer und Herbst) erfasst. Fünf Jahre nach dem Beginn der experimentellen Fragmentierung gab es keine Dichteunterschiede bei *B. officinalis* Rosetten in Fragmenten und Kontrollflächen. *B. officinalis* produzierte aber mehr Blätter per Rosette in Fragmenten als in Kontrollflächen, allerdings nur im Sommer. Die Frassschäden, ausgedrückt als Anteil der durch Herbivoren entfernten Blattfläche, nahmen während der Vegetationsperiode zu und waren an zwei Standorten grösser in Fragmenten als in Kontrollflächen. Am dritten Standort waren sie kleiner in Fragmenten (allerdings weniger deutlich). Die Artenzahl und die Dichten (Individuen pro m²) potentieller Herbivoren (Gastropoden und Heuschrecken) wurden in allen Fragmenten und Kontrollflächen erfasst. Fragmentierungseffekte auf die Artenzahl und die Herbivorendichte waren abhängig von der Plotgrösse und unterschiedlich für Gastropoden und Heuschrecken. Das Ausmass der Fraßschäden in Fragmenten nahm mit steigender Gastropodendichte zu, wenn der dritte Standort, der die geringsten Frassschäden aufwies, ausgeschlossen wurde. Solch eine positive Beziehung wurde weder in Kontrollflächen noch für die Heuschreckendichten gefunden. Die Mobilität der Gastropoden in Fragmenten wurde möglicherweise eingeschränkt was zumindest an zwei Standorten zu einem höheren Herbivorendruck führte. Die Interpretation der experimentellen Resultate ist aber schwierig, denn obwohl das Experiment ein gutes Design und genügend Replikate hatte, war die Variabilität zwischen den Standorten und Jahreszeiten gross.

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Introduction

Habitat fragmentation alters naturally existing landscapes and affects numerous ecological processes across multiple spatial scales (Kareiva & Wennergren, 1995; Saunders, Hobbs, & Margules, 1991; Schweiger, Diffendorfer, Holt, Pierotti, & Gaines, 2000; Zschokke et al., 2000). The total area available to organisms is reduced and the remaining habitat is broken up into more or less isolated fragments. As a result of the decreased area of these remnants, population sizes are reduced, leading to a higher risk of disappearance of some species due to stochastic events (Berwaerts, van Dyck, van Dongen, & Matthysen, 1998; Ebenhard, 1995; Fischer, van Kleunen, & Schmid, 2000; Kery, Matthies, & Schmid, 2003; Lienert, Diemer, & Schmid, 2002). Fragmentation changes habitat characteristics and influences population and community dynamics through the increased impact of external factors such as physical disturbances, predation and parasitism (Goverde, Schweizer, Baur, & Erhardt, 2002; Kruess & Tschardtke, 1994; Lord & Norton, 1990). These may be accompanied by less obvious, indirect effects. For example, if fragmentation affects the distribution and abundance of insects, the resource base of insectivorous

birds may be altered (Wiens, 1994). Thus, habitat fragmentation can influence an entire suite of processes, ranging from individual behaviour through population dynamics to ecosystem fluxes.

Grazing animals are important in community organisation in different types of habitats (Crawley, 1997; Strauss & Agrawal, 1999). Several studies demonstrate effects of herbivory on plant fitness, including timing of seed production, number and size of seeds and seedling establishment (Crawley & Nachapong, 1985; Hawkes & Sullivan, 2001; Tiffin, 2002). However, relatively little is known about the effect of habitat fragmentation on abundance and diversity of herbivores, especially for invertebrate phytophagous species (Didham, Ghazoul, Stork, & Davis, 1996). Few studies have investigated the effect of fragmentation on insect herbivores. For example, increasing isolation reduced the diversity and density of stem borers and seed feeders of red clover, *Trifolium pratense* (Kruess & Tschardtke, 1994). The density of the herbivorous flea beetle *Phyllotreta cruciferae* was reduced in experimentally fragmented broccoli fields compared to fields with low level of fragmentation (Banks, 1998). In contrast, little or no effects of fragmentation on species richness and abundance were found in stem-boring insects of fragmented *Calamagrostis*

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