GfÖ Ecological Society of Germany, Austria and Switzerland

Basic and Applied Ecology 15 (2014) 347–352

Basic and Applied Ecology

www.elsevier.com/locate/baae

Invertebrate herbivory decreases along a gradient of increasing land-use intensity in German grasslands

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Received 21 July 2013; accepted 20 March 2014
Available online 29 March 2014

Abstract

Land use is a major driver of biodiversity loss in many taxa including species-rich invertebrate assemblages, but consequences for invertebrate-mediated processes are still little studied. We assessed invertebrate herbivory in 146 managed temperate grasslands across a broad range of land-use intensities in three regions of Germany. Average herbivory decreased with increasing land-use intensity independent of region from 1.3 to 0.4% leaf area assessed. Among grassland land-use practices, the frequency of mowing and the degree of fertilization decreased herbivory while the intensity of vertebrate grazing had no significant effect on invertebrate herbivory. Thus, grassland management not only affects the diversity and abundance of invertebrate assemblages but also the amount of leaf tissue consumed.

Zusammenfassung

Landnutzung ist eine der Haupttriebkräfte für den globalen Biodiversitätsverlust einschließlich der artenreichen Invertebratengemeinschaften, die Konsequenzen für durch Invertebraten vermittelte Prozesse sind jedoch wenig untersucht. Wir erfassten Invertebraten-Herbivorie in 146 bewirtschafteten temperaten Grasländern über ein breites Spektrum unterschiedlicher Nutzungsintensität in drei Regionen Deutschlands. Die durchschnittliche Herbivorie nahm mit zunehmender Nutzungsintensität unabhängig von der Region von 1,3 auf 0,4 Prozent der erfassten Blattfläche ab. Von den untersuchten Landnutzungskomponenten beeinflussten Mahdfrequenz und Düngung die Invertebraten-Herbivorie negativ während die Stärke der Beweidung keinen signifikanten Effekt auf die Invertebraten-Herbivorie zeigte. Somit beeinflusst das Grasland-Management nicht nur die Diversität und Abundanz von Invertebratengemeinschaften, sondern auch die Menge an konsumiertem Blattgewebe.

Keywords: Ecosystem process; Grassland management; Mowing; Grazing; Fertilization; Insects

Introduction

Land use is a main driver of changes in biodiversity and ecosystem processes (Foley et al. 2005). Invertebrates, in particular insects, are the most diverse group of multicellular organisms in terrestrial habitats and mediate a number

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http://dx.doi.org/10.1016/j.baae.2014.03.003
1439-1791/

of important ecosystem functions (reviewed in Weisser & Siemann 2004a). Most biodiversity studies that focus on invertebrates do, however, concentrate on the consequences of land use on insect diversity rather than on processes mediated by insects (e.g. Hendrickx et al. 2007). A general result from these studies is that increasing land-use intensity decreases invertebrate abundance and diversity (Attwood, Maron, House, & Zammit 2008) where in particular insects and molluscs, are expected to suffer from land use often indirectly due to reduced plant species diversity (Siemann 1998).

Studies on the consequences of increasing land use on invertebrate-mediated processes have mainly focused on pollination documenting a loss in pollinator species which in turn resulted in decreased pollination for a range of plant species including important crops in various habitats (e.g., Garibaldi et al. 2013). In contrast, consequences of land use for other invertebrate-mediated processes such as herbivory are less investigated (reviewed in Schowalter, Hargrove, & Crossley 1986; Tscharntke & Greiler 1995; Norris & Kogan 2005), even though this ecosystem process affects many other ecosystem functions such as nutrient cycling and plant productivity (Hartley & Jones 2004). Although invertebrate herbivory levels in grasslands are generally low (10% or less; Weisser & Siemann 2004b; Unsicker et al. 2006), for the plants involved, such insect herbivory may be significant. This is supported by the many anti-herbivore adaptations and by studies that manipulate plant defense, which showed that herbivory would be much higher if plants did not invest as much in defense (Kessler, Halitschke, & Baldwin 2004). In addition, effects on nutrient cycling may be significant, even at low levels of herbivory (Hunter 2001; Stadler, Solinger, & Michalzik 2001; Kessler, Halitschke, & Baldwin 2004).

The reduction in abundance and diversity in the herbivorous invertebrate community by increasing land-use intensity, e.g. due to direct mowing effects, is expected to result in reduced herbivory because fewer herbivores are expected to consume less biomass. Indirect effects are mediated via changes in the plant community. Different predictions for the direction of indirect effects of land use on herbivory can be made based on the results and theory of biodiversity functioning research. Under the settings of most biodiversity-ecosystem function experiments with their standardized fertilization levels, lower herbivory can be expected in the less productive, species poor plant assemblages (e.g. Hector et al. 1999). This is due to a decreasing herbivore abundance (more individuals hypothesis; Srivastava & Lawton 1998), in particular of generalists among them (e.g., Schuldt et al. 2012; Loranger et al. 2013a). On the other hand reduced plant diversity might result in increased herbivory, at least by specialist herbivores. This might be caused either by an increased abundance of suitable plant host species (resource concentration; Root 1973) or due to higher nutrient concentrations (e.g. amino acid) and consequently higher palatability of plant material as a consequence of fertilization (Tylianakis, Didham, Bascompte, & Wardle 2008). In real-world grasslands with intermediate to high land-use intensity the relationship between plant species richness and productivity is usually opposite. There, higher intensity increases net primary productivity (NPP) and reduces plant species richness (e.g. Harpole & Tilman 2007). This is most likely due to competition for light in highly productive stands (e.g. Hautier, Niklaus, & Hector 2009).

In this paper we investigate how aboveground invertebrate herbivory is affected by land-use intensity, using grasslands as a model system. By assessing a large number of differently managed grasslands including meadows, pastures and mown pastures, we also aim to identify if these management components differently affect invertebrate herbivory in grasslands.

Materials and methods

Study sites and grassland land use

The study was conducted in three regions of Germany within the Biodiversity Exploratory project (www.biodiversity-exploratories.de; Fischer et al. 2010): (1) The biosphere reserve Schorfheide-Chorin in north-east Germany (3–140 m a.s.l., 53°02′N 13°83′E, annual mean precipitation 500–600 mm, mean temperature 8–8.5 °C). (2) The National Park Hainich and the surrounding Hainich-Dün area in central Germany (285–550 m a.s.l., 51°20′N 10°41′E, 500–800 mm, 6.5–8 °C). (3) The biosphere reserve Schwäbische Alb in south-west Germany (460–860 m a.s.l., 48°43′N9°37′E, 700–1000 mm, 6–7 °C). In each region, 50 grasslands (meadows, pastures grazed by different kinds of livestock, i.e. cattle, sheep or horses, or both mown and grazed grasslands: mown pastures) were included in the study. On some of these grasslands fertilizer was applied in different amounts. Thus, plots (sizes of 50 m × 50 m) covered the complete range of grassland land-use intensities in the regions. Management practices on the grasslands were assessed each year by standardized interviews with the land-owners. From these interviews, information on fertilization, grazing and cutting were derived (see Blüthgen et al. 2012). Briefly, fertilization intensity was calculated as the total amount of nitrogen (kg) applied per hectare, in the form of chemical fertilizer, manure or slurry. For grazing, information on livestock units and the duration of grazing periods were combined as a measure of grazing intensity. Cutting intensity was included as the number of cutting events. We additionally integrated the three components into the regionally standardized land-use intensity measure LUI (see Blüthgen et al. 2012). Mean LUI for the years 2006–2010 was calculated (see Appendix A).

Herbivory measurements

We assessed herbivory on all plots in May 2013, before any of the grasslands was mown, as this is the only