Science of the Total Environment 644 (2018) 60–67

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Direct and indirect effects of land use on bryophytes in grasslands

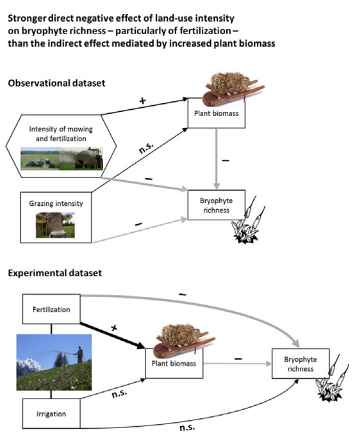
Steffen Boch [a,b,*], Eric Allan [b], Jean-Yves Humbert [c], Yasemin Kurtogullari [b,c], Malie Lessard-Therrien [c,f], Jörg Müller [d], Daniel Prati [b], Nora Simone Rieder [b,c], Raphaël Arlettaz [c,e], Markus Fischer [b]

[a] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
[b] Institute of Plant Sciences, University of Bern, Altenbergrain 21, 3013 Bern, Switzerland
[c] Division of Conservation Biology, Institute of Ecology and Evolution, University of Bern, Baltzerstrasse 6, 3012 Bern, Switzerland
[d] Department of Nature Conservation, Heinz Sielmann Foundation, Unter den Kiefern 9, 14641 Wustermark, Germany
[e] Swiss Ornithological Institute, Valais Field Station, Rue du Rhône 11, 1950 Sion, Switzerland
[f] College of Biological Science, University of Guelph, 50 Stone Road East, Guelph, Ontario, Canada

HIGHLIGHTS

- Land-use intensification strongly reduces bryophyte richness and cover.
- Direct land-use effects are larger than indirect ones via increased plant biomass.
- In particular fertilization has the strongest negative effect on bryophytes.
- Limited fertilizer input is crucial to maintain bryophyte diversity in grasslands.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 4 April 2018
Received in revised form 26 May 2018
Accepted 26 June 2018
Available online xxxx

Editor: R Ludwig

Keywords:
Fertilization
Grassland biodiversity
Land-use intensification
Liverwort
Moss
Structural equation modelling

ABSTRACT

Land-use intensification is the major threat for biodiversity in agricultural grasslands, and fertilization has been suggested as the most important driver. A common explanation for the decline of bryophyte diversity with higher land-use intensity is an indirect negative effect via the increase in vascular plant productivity, which reduces light levels for bryophytes. However, direct negative effects of land-use intensification may also be important. Here, we disentangle direct and vascular plant biomass mediated indirect effects of land use on bryophytes. We analyzed two complementary datasets from agricultural grasslands, an observational study across 144 differently managed grasslands in Germany and an experimental fertilization and irrigation study of eleven grasslands in the Swiss Alps. We found that bryophyte richness and cover strongly declined with land-use intensity and in particular with fertilization. However, structural equation modelling revealed that although both direct and indirect effects were important, the direct negative effect of fertilization was even stronger than the indirect effect mediated by increased plant biomass. Thus, our results challenge the widespread view that the negative effects of fertilization are mostly indirect and mediated via increased light competition with vascular plants. Our study shows that land use intensification reduces bryophyte diversity through several different mechanisms. Therefore, only low-intensity management with limited fertilizer inputs will allow the maintenance of bryophyte-rich grasslands.

* Corresponding author at: Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland.
E-mail address: steffen.boch@wsl.ch (S. Boch).

https://doi.org/10.1016/j.scitotenv.2018.06.323
0048-9697/

1. Introduction

Extensively managed grasslands harbor a high diversity of many different taxa (Allan et al., 2014). However, on the majority of agricultural grasslands this diversity is threatened by land-use intensification (e.g., Kleijn et al., 2008; Allan et al., 2014; Gossner et al., 2016). With the aim to increase yield, semi-natural grasslands often receive large amounts of organic or inorganic fertilizer, often in combination with irrigation in drier regions. This results in long-term changes in species composition and in biodiversity loss (Humbert et al., 2016; Melts et al., 2018). In addition, these productive grasslands are mown more frequently or are grazed at higher stocking densities than in the past (Blüthgen et al., 2012). While these effects of land-use intensification on the diversity of vascular plants have been well studied (e.g., Kleijn et al., 2008; Socher et al., 2012), bryophytes have only rarely been considered. However, bryophytes a group including mosses, liverworts and hornworts, are often abundant in grasslands, where they constitute a substantial part of the total grassland plant diversity (Dengler et al., 2006, 2016) and contribute to several important ecosystem processes such as C and N cycles (Turetsky, 2003). As diversity, but also the abundance, of multiple taxa, including locally rare species, is important to maintain ecosystem functions (e.g. Soliveres et al., 2016a, 2016b), the loss of bryophyte diversity and abundance could lead to reduced ecosystem functioning in grasslands. Moreover, bryophyte diversity is a very good indicator of the overall diversity of grasslands (multidiversity), and the diversities of many individual plant and animal taxa (Manning et al., 2015). Understanding land-use effects on bryophytes is therefore important to better preserve this important group and to maintain basic ecosystem functions.

A number of observational and experimental studies have shown a negative relationship between bryophyte richness and vascular plant cover or grassland productivity, and that fertilization is one of the main drivers reducing bryophyte species richness and cover in grasslands (Jäppinen and Hotanen, 1990; Carroll et al., 2000; Bergamini and Pauli, 2001; Aude and Ejrnæs, 2005; Bobbink et al., 2010; Verhoeven et al., 2011; Müller et al., 2012; Boch et al., 2015; van Klink et al., 2017). Most of these studies have assumed that the main mechanism driving the decline in bryophytes is an increase in vascular plant biomass, which reduces light levels for low growing bryophytes. Both experimental (Hautier et al., 2009; DeMalach and Kadmon, 2017; DeMalach et al., 2017) and observational studies (Grace et al., 2016) have shown that an increase in light competition is the major driver of reduced plant diversity at high productivity. However, a loss of resource niches could also contribute to reducing plant diversity in fertilized conditions (reduced niche dimensionality hypothesis: Harpole and Tilman, 2007; Harpole et al., 2017). Fertilization may also reduce plant diversity via other mechanisms, such as toxicity and acidification (Bobbink et al., 2010) and these direct negative fertilizer effects (in particular by ammonia) may also be important for bryophytes (Jäppinen and Hotanen, 1990; Carroll et al., 2000; Krupa, 2003; Pearce et al., 2003; Paulissen et al., 2004; Du et al., 2014; Andersen et al., 2016; Sun et al., 2017). Moreover, fertilization effects depend on the physicochemical environment and may interact with other components of land use. For instance, in drier regions fertilization requires increased levels of irrigation to be effective, which may in turn also directly affect bryophyte diversity (Mamolos et al., 2005). The relative importance of these direct fertilization effects, mediated by changes in soil chemistry, compared to indirect effects mediated through changes in plant productivity and light levels is not known.

Traditional land-use management, such as extensive mowing or grazing, is important for maintaining semi-natural temperate grasslands and their diversity because it prevents shrub encroachment and increase light levels for subordinate plant species (Pykälä, 2005; Hejcman et al., 2013; Borer et al., 2014). However, increased mowing frequency – which generally occurs together with greater fertilizer inputs – leads to a homogenous sward and can reduce grassland diversity, including bryophyte diversity (e.g. Müller et al., 2012; Allan et al., 2014). The effect of grazers is even more complex, as grazing removes biomass but also results in trampling and the deposition of dung as well as urine. This creates habitat heterogeneity in terms of unevenly deposited nutrients and sward cover and the trampling creates open soil patches which provide microsites for seedling recruitment (Oldén et al., 2016). However, similar to mowing, high grazing pressure can homogenize grasslands and reduce their overall diversity (e.g. Pykälä, 2005; Allan et al., 2014). This means that grazing could have several direct effects on bryophyte diversity, along with indirect effects mediated by changes in plant biomass.

The aim of this study was to determine the importance of direct and indirect land-use effects for bryophytes. For this, we used structural equation modelling (SEM; Shipley, 2002) which is a powerful statistical tool in well-replicated comparative studies. Some studies have used SEM to separate direct and indirect effects of fertilization, mowing and grazing on vascular plant diversity (e.g., Socher et al., 2012), but this approach has only very rarely been used for studies on bryophytes (but see Spitale et al., 2009). We fitted SEMs to two datasets: the first is a large-scale observational dataset from the Biodiversity Exploratories project, which includes 150 grasslands in three regions of Germany differing in land-use intensity. The second is a dataset from the Swiss Alps, in which fertilization and irrigation were experimentally manipulated at various intensity levels in semi-natural grasslands. We hypothesized that increasing fertilization, and also irrigation, should increase the biomass production of vascular plants, and thereby decrease bryophyte richness and cover indirectly via increased light competition. We expected this indirect effect to be stronger than the direct effects of fertilization. As increasing intensities of mowing and grazing cause frequent disturbance and are only done on productive grassland, we expected them to reduce bryophyte species richness and cover, even though plant biomass is removed.

2. Methods

2.1. Study sites, land use and vegetation

We used two complementary datasets to investigate land-use effects on bryophytes. The first dataset (called the observational dataset, henceforth) contains observational data on bryophyte species richness along a land-use intensity gradient in German grasslands (the German Biodiversity Exploratories; Fischer et al., 2010). The second dataset (called the experimental dataset, henceforth) contains experimental data on bryophyte species richness from a replicated field experiment that tested the effects of modern fertilization and irrigation upon plant and invertebrate communities of Swiss mountain hay meadows, with the objective to define optimal trade-offs for sustainable grassland management (e.g., Andrey et al., 2016; Lessard-Therrien et al., 2017). Combining these two datasets therefore allowed us to generalize findings across a range of different grassland types and to assess i) how intensification of land-use components affects bryophyte species richness and ii) how important direct intensification effects on bryophyte species richness are, compared to plant biomass-mediated indirect ones (see details below). Nomenclature of bryophytes follows Koperski et al. (2000).

2.2. The observational dataset from the German Biodiversity Exploratories project

The Biodiversity Exploratories comprise 150 grassland sites situated in three regions of Germany: the UNESCO Biosphere area Schwäbische Alb (Swabian Jura), situated in a low mountain range in South-western Germany, the National Park Hainich and its surrounding areas, situated in the hilly lands of Central Germany, and the UNESCO Biosphere Reserve Schorfheide-Chorin, situated in the young glacial lowlands of North-eastern Germany. The three regions differ in climate,