Direct and indirect effects of land use on bryophytes in grasslands

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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.

Keywords

Fertilization, grassland biodiversity, land-use intensification, liverwort, moss, structural equation modelling

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, geology and topography (Tab. 1). The gradients of land use and species pools are typical for the variation found among large parts of temperate lowland Europe. Plots were selected to differ strongly in land-use intensity, whilst minimizing confounding with soil conditions or space (for details see Fischer et al., 2010; Blüthgen et al., 2012).

In 144 of these grassland sites, we recorded the species richness of terricolous bryophytes (species growing on soil) and estimated the percentage cover per species in 4 m × 4 m plots in summer 2007 and 2008. Information on land-use intensity was obtained via questionnaires sent to farmers and land owners. Our plots included meadows (mown one to four times per year for hay or silage production), pastures grazed by livestock at different densities (sheep, cattle or horses), or grasslands which were mown once per year and grazed by livestock at different densities, the so-called mown pastures. Grazing regimes differ among livestock types: sheep-grazed pastures are rotational or grazed by traditional shepherding (minimum is two grazing days per year) but pastures grazed by cattle or horses are mainly permanent (up to 240 grazing days per year). Plots were either unfertilized, or fertilized to different extents (Fischer et al., 2010; Boch et al., 2016a). We quantified land-use intensity (LUI) using an integrated measure, which sums up the standardized intensities of fertilization (kilograms of nitrogen per hectare per year), mowing (number of cuts per year) and grazing (duration and type of grazing animals, converted to livestock units), calculated as:

$$LUI[i] = \sqrt{\frac{F[i]}{F_{mean}} + \frac{M[i]}{M_{mean}} + \frac{G[i]}{G_{mean}}}$$

where F_{mean}, M_{mean} *and* G_{mean} are mean values of all 50 plots of each study region (for details see Blüthgen et al., 2012). For example, a very low LUI of 0.5 can be achieved through 30 days of grazing per ha by one cow, an intermediate LUI of 1.5 corresponds to a meadow which is mown twice and receives 60 kg N per year, and a relatively high LUI of 3.0

corresponds to a meadow which is mown three times and receives 130 kg N per year (Boch et al., 2016b).

Other studies compared the performance of the overall LUI (with equal weighting of components) to models with grazing, fertilization and mowing fitted separately (where the components can vary in the strength and direction of effect) and showed that LUI was a better predictor of several diversity measures (including bryophyte diversity) than the individual components, indicating its robustness and the validity of considering equal effects of the land use components (Blüthgen et al., 2012; Allan et al., 2014).

We also sampled aboveground vascular plant biomass (plant biomass hereafter), to assess annual grassland productivity, by clipping the vegetation at a height of 5 cm in eight 50 cm × 50 cm subplots. These subplots were adjacent to the plots in which we recorded bryophytes. In meadows, we sampled plant biomass at the same time as the first hay harvest by the farmer. In pastures and mown pastures, we temporarily fenced our subplots to ensure that the vegetation had not been grazed before plant biomass sampling. The plant biomass samples were pooled, dried for 48 h at 80 °C and weighed immediately after drying.

2.3 The experimental dataset from the Swiss mountain hay meadows

The second, experimental dataset originates from the canton of Valais in southwestern Switzerland and contains data from semi-natural grasslands differing markedly from the German ones in terms of altitude and climate (Tab. 1). In 2010, eleven extensively managed meadows were selected, which were at least 4000 m^2 in size, had received no or very low levels of fertilizer (only solid manure), and/or were irrigated during droughts before the onset of the experiment, and had been mown once a year for at least the past ten years.

In each meadow, six circular plots with a diameter of 20 m were established with at least 5 m between plots as buffer zone. Then, six different management treatments were randomly assigned to the six plots and applied consistently in each plot for five years. The treatments were control, irrigation only (medium intensity), fertilization only (medium intensity), and a combination of both irrigation and fertilization at three different intensity levels (low, medium, high). In these, amounts varied from 1/3, through 2/3 to 3/3 of the quantity theoretically needed to achieve maximum hay yield, under local conditions and a mowing regime consisting of two hay harvests per year. From mid-May to the beginning of September sprinkler irrigation was applied weekly with 10, 20 or 30 mm of water added, depending on the intensity level of the irrigation treatment. The plots were not irrigated when >20 mm rain had fallen in the previous week. Twice per year, in spring and after the first hay harvest, the fertilized plots received a water-dissolved solution of organic dried manure NPK pellets (MEOC SA, 1906 Charrat, Switzerland) and mineral potassium-sulphate (K_2SO_4), corresponding to the standard-farm liquid manure (2.4 kg N, 2 kg P_2O_5, and 8 kg K_2O per m^3 of solution; according to Sinaj et al., 2009). The total amount of added fertilizer (kg N $ha^{-1}year^{-1}$) depended on the theoretical local hay production potential, calculated from pre-experimental hay yield and site altitude (for details see Appendix A in Andrey et al., 2016).

In July 2015, we sampled all terricolous bryophyte species and estimated the percentage cover per species in a 2 m × 4 m subplot within each of the 66 treatment plots. In addition, the productivity of each plot was quantified twice; once before each hay harvest by the farmer. Productivity was assessed by clipping the vegetation at a height of 6 cm in two 1.6 m^2 rectangle subplots, adjacent to the plots in which we recorded bryophytes. Then, the two samples were pooled, dried at 105°C for 72 h and weighed.

2.4 Statistical analysis

All statistical tests were performed using R, version 3.2.4 (R Core Team, 2016). We used linear mixed-effect models (lme4 package; Bates et al., 2015) to test effects of land-use components and land-use intensity (LUI; observational dataset), amount of added fertilizer and amount of added water (experimental dataset) on plant biomass production and bryophyte richness.

When analyzing the observational grassland dataset, we included region with three levels as a random factor and the land-use components as fixed factors. However, disentangling the relative effects of the land-use components on bryophyte richness, bryophyte cover and vascular plant biomass was not possible as mowing and fertilization intensity were strongly confounded (both factors increase plant biomass and reduce bryophyte species richness and cover; results are not shown). This is because fertilized grasslands are always mown more frequently. Therefore, we calculated a combined fertilization and mowing intensity measure, summing up the standardized intensities of fertilization and mowing (see above for details on LUI calculations; Tab. 2) and fitted it together with grazing intensity. In addition, we fitted a separate model with the compound LUI as a fixed factor and region as a random factor. As this analysis yielded qualitatively similar results (Tab. A.1), we do not discuss it further.

For the experimental dataset, we fitted study site (11 levels) as a random factor to correct for differences among sites. We included irrigation (amount of added water; mm/week) and fertilization (amount of added nitrogen; kg N $ha^{-1}year^{-1}$) as continuous fixed effects. We also included altitude as a co-variate and further tested its interaction with fertilizer, to test whether fertilizer had different effects at different altitudes. The interaction between fertilizer and altitude was never significant, so we excluded it from the final analysis and we do not discuss it further. Fitting the experimental treatments as a categorical fixed factor instead of the continuous fixed effects of fertilization and irrigation yielded qualitatively similar results, so we do not discuss the results of the categorical fixed factor analysis further.

We further used structural equation modelling (SEM) to evaluate the direct and indirect effects of increased LUI, as well as increased intensity of the land-use components (fertilization, mowing and grazing separately; observational dataset) and treatment effects (fertilization and irrigation; experimental dataset) on bryophyte richness. We first developed an *a priori* model based on the known effects and relationships among the drivers of bryophyte diversity. To avoid large differences in the variances among the factors and to improve model convergence, we standardized all variables to a mean of 0 and standard deviation of 1. Moreover, we tested the bivariate relationships between all variables to ensure that a linear model was appropriate.

In the observational dataset, we first corrected for regional differences by fitting a linear model with region as a fixed factor to the species richness of bryophytes and the vascular plant biomass. We then used residuals in subsequent analyses for estimating path coefficients, using the lavaan package (Rosseel, 2012). As the land-use components fertilization, mowing and grazing were already regionally standardized (see above), we used these values for further analysis. As mowing (cutting frequency) and fertilization intensity were strongly confounded (see explanation above) we introduced a composite variable into our model, which summarises the combined effects of mowing and fertilization intensity. The use of composite variables does not alter the SEM model but collapses the effects of conceptually related variables into a single composite effect (Grace, 2006). As some variables were not perfectly normally distributed, we confirmed the fit of the model using bootstrapping with 1000 iterations. We also tested the direct and indirect effect of the integrated measure of LUI on bryophyte species richness in a separate analysis. As the analysis yielded qualitatively similar results (Supplementary material Fig. A.1) but was less informative because the effect of grazing is not separated from the combined fertilization and mowing effect, we do not discuss the results further.

In the experimental dataset, we estimated path coefficients by calculating a piecewise SEM with maximum likelihood estimation, using the piecewise SEM package (Lefcheck, 2015). This is a useful tool for simultaneously testing complex multivariate hypotheses, using a set of linear mixed-effect models, as it allows the inclusion of random factors. For the experimental dataset, we included study site as a random factor in the underlying mixed models. As our *a priori* model for the experimental dataset was saturated – i.e. there was a direct uni- or bi-directional relationship between all variables, because all were plausible hypotheses – it was not possible to perform the traditional goodness-of-fit test for the model.

3. Results

3.1 Land-use effects on plant biomass, bryophyte species richness and bryophyte cover

Land-use intensification strongly reduced bryophyte richness and cover. In the observational dataset, low LUI plots (LUI <1.5; N = 60) harbored on average 3.9 (± 0.5 SE) bryophyte species, while high LUI plots (LUI >1.5plots; N = 84) harbored 1.8 (± 1.4) species. Bryophyte cover was on average 13.7% (± 2.3 SE) in low LUI plots, while in high LUI plots it was only 2.1% (± 0.1).

In the experimental dataset, mean bryophyte species richness ranged from an average of 9.8 (± 1.1) in the control plots to 3.1 (±0.4) in the high intensity plots. Bryophyte cover ranged from an average of 22.1% (± 7.3) and 26.0% (± 7.3) in the control and irrigation plots, respectively, to 4.6% (± 1.9) in the high intensity plots.

In our linear models, plant biomass generally increased while bryophyte species richness and cover decreased with increasing mowing-fertilization intensity (observational dataset; Tab. 2; Supplementary material Fig. A.2; see also Tab. A.1 and Fig. A.3 for effects of increasing LUI), and with higher amounts of added fertilizer (experimental dataset; Tab. 2;

Supplementary material Fig. A.4). Moreover, increasing grazing intensity also reduced bryophyte species richness (observational dataset; Tab. 2). In the experimental dataset, we found no effects of altitude and irrigation on plant biomass and bryophyte species richness (Tab. 2; Fig. A.4).

3.2 Direct versus indirect land-use effects on bryophyte species richness

Land-use intensity had larger direct than indirect effects on bryophytes. In the observational dataset, the structural equation modelling shows that the cumulative direct effect of fertilization and mowing intensity (land-use intensity composite variable) on bryophyte species richness was strongly negative and even stronger than the indirect effect mediated by increased plant biomass (standardized effects: -0.37 vs. -0.05; Fig. 1A). In addition, we found a moderate, negative effect of grazing intensity on bryophyte species richness.

In the experimental dataset, fertilization also directly decreased bryophyte species richness, and this direct effect was again stronger than the indirect effect mediated by increased plant biomass (-0.54 vs. -0.16; Fig. 1B). Irrigation, in contrast, had no direct or indirect effect on bryophyte species richness.

4. Discussion

To increase productivity, grasslands are commonly fertilized and in dry areas, such as the inner-alpine valleys of the Valais (SW Switzerland), they are often irrigated. As a result, these grasslands can be mown more frequently or grazed with higher livestock densities. These aspects of land-use intensification all seem to reduce grassland bryophyte species richness. The one exception is irrigation, which had no effect on bryophyte species richness in the Swiss Alps, which supports results from Müller et al. (2016) who found no effects of irrigation on plant species richness in German lowland grasslands. Moreover, in our study irrigation had no significant effect on bryophyte cover. This is in contrast to Virtanen et al. (2017) who found an increasing bryophyte cover in only irrigated experimental plots under Mediterranean climate conditions in California. However, high rates of fertilization seem to be particularly negative for bryophytes.

In line with a number of other studies, we observed an overall decrease in bryophyte species richness and cover with increasing fertilization. In particular, only very few species remained, and at low abundance in strongly fertilized plots, such as *Eurhynchium* species or large-growing *Brachythecium* species, which are known to tolerate fertilization (Dirkse and Martakis, 1992; Nebel and Philippi, 2001). Other less competitive species suffered from even very low amounts of fertilizer and were absent in our fertilized plots (e.g. *Aphanorrhegma patens, Campylium calcareum*, *Ditrichum cylindricum*, *Leptobryum pyriforme, Phascum* spp., *Pottia* spp., *Pterygoneurum ovatum*). In addition, all 15 species listed as endangered or near threatened in Germany (see Ludwig et al., 1996: *Campylium calcareum, C. chrysophyllum, Ctenidium molluscum, Didymodon acutus, Rhytidium rugosum, Entodon concinnus, Fissidens dubius, Homalothecium lutescens, Hylocomium splendens, Rhytidiadelphus triquetrus, Thuidium abietinum, T. philibertii, Tortella tortuosa, Weissia brachycarpa, W. longifolia var. longifolia*) occurred only in unfertilized plots, with a LUI below 1.5. *Homalothecium lutescens* was present at low abundance in two plots and *Tortella tortuosa* in one plot with low fertilizer input. Our results agree with several other observational and experimental studies: Virtanen et al. (2000), working in the long-term Park Grass experiment in England, and Bergamini and Pauli (2001), working in Swiss calcareous fens, both found a decline in bryophyte richness with increasing fertilizer application. Müller et al. (2012) also observed a decrease in bryophyte richness with increasing productivity, along a land-use intensity gradient in German grasslands. Virtanen et al. (2017) found a reduction of bryophyte species richness and cover in experimental plots, which were irrigated and fertilized. However, these previous studies were not able to identify the mechanisms behind the impacts of fertilization.

By using SEM, we could separate direct fertilization, irrigation and grazing effects from the indirect effects that are mediated by an increase in plant biomass, to better understand the mechanisms underlying the effect of fertilization on bryophytes. Interestingly, we found that the direct negative effect of fertilization and mowing in the observational dataset and fertilization in the experimental dataset, was even stronger than the indirect negative effect caused by increased plant biomass. The direct effects of fertilization could be explained by the toxic effects of nitrogen: during the mineralization process, organic material or fertilizer is first transformed into ammonia (ammonification) by saprobiotic bacteria, then to nitrite and finally to nitrate by nitrifying bacteria (nitrification). While the enrichment of terrestrial systems with nitrate mainly increases productivity (Humbert et al., 2016), the addition of ammonia can have direct toxic effects on plants (e.g., disturbance of the ionic balance in leaves, decreasing their longevity and growth: Roelofs et al., 1985). Bryophytes lack true roots and vascular systems and therefore take up water and nutrients across their whole surface, which may make bryophytes more sensitive to toxic fertilizer effects. Such toxic fertilizer effects, in particular from ammonia, have been identified in experiments on selected moss species (Krupa, 2003; Pearce et al., 2003; Paulissen et al., 2004, Andersen et al., 2016). For example, Krupa (2003) reviewed effects of atmospheric ammonia on plants and reported foliar damage on four moss species. Paulissen et al. (2004) and Andersen et al. (2016) reported direct negative effects of ammonia on fen bryophyte species investigated in greenhouse experiments. In addition, Verhoeven et al. (2011) found negative effects of ammonia on bryophyte species richness in an experimental study from a fen in Ireland and suggested a combination of increased competition with vascular plants and direct toxic fertilizer effects as the two main causes.

In addition to these direct effects, fertilization did also indirectly reduce bryophyte species richness by increasing plant biomass. In all our study grasslands, plant biomass clearly increased with land-use intensification and in particular with larger fertilization inputs. This increase of plant growth and plant biomass following fertilization causes a loss of plant diversity, principally due to increased light competition and the shading out of understory plants by taller species (Hautier et al., 2009; Grace et al., 2016; DeMalach et al., 2017). The understory layer of grasslands, below the vascular plant canopy, is often formed of bryophytes. If we assume that plant biomass negatively correlates with the light available for bryophytes, our results suggest that an increase in light competition from vascular plants partially explains the negative effect of fertilization on bryophyte diversity. Feßel et al. (2016), who measured light transmittance to the ground in German grasslands, found sward cover and aboveground biomass – two positively related factors (Heer et al., 2018) – to be the most important factors explaining lower light levels on the ground, supporting our assumption that higher biomass means less light. Our results indicate that fertilization affects bryophyte diversity through several mechanisms and that the impacts may be more complex than previously thought.

The type of fertilizer may also be important and different fertilizers may vary in how much they reduce bryophyte diversity. In our plots, both in the experimental and in the observational study, liquid manure was the main type of added fertilizer, which consists of solid particles with high nutrient concentrations that cover the vegetation until the next rain event. It has been demonstrated that these solid components can directly kill bryophytes by osmotic effects, leading to so-called “browning” and this can strongly reduce their cover (Jäppinen and Hotanen, 1990). The underlying physiological mechanism of these toxic effects of fertilizer on bryophytes certainly needs more detailed, experimental investigations to be fully understood. However, our results already suggest that these effects are even more important than the increased light competition by vascular plants in reducing bryophyte diversity in intensively managed grasslands.

In the observational dataset, we found decreased bryophyte species richness at high land-use intensity and that intensive grazing and mowing also reduced bryophyte diversity. Disturbances caused by intensive mowing and grazing could therefore also contribute to the decline of bryophyte species richness in intensively managed grassland: against the intuitive expectation that higher mowing frequencies might be positive for bryophytes, because it reduces plant cover and thereby increases the light levels at the ground, Müller et al. (2012) found that bryophyte richness declined with increasing mowing frequency. However, as frequently mown plots were also fertilized, it might well be that that this effect was driven by the direct negative fertilizer effect. High grazing intensity can also reduce bryophyte richness because of trampling and eutrophication (Pearce et al., 2010; Ludvíková et al., 2014), however it is likely that low-intensity grazing would promote the highest bryophyte species richness (Bergamini et al., 2001). This is probably due to the enhanced environmental heterogeneity promoted by light grazing and because grazing animals increase light levels by removing of vascular plant biomass (Borer et al., 2014). Other studies have also found positive effects of grazing on bryophytes, for example Takala et al. (2014) found that cattle grazing increased bryophyte species richness in Finnish semi-natural grasslands. We do not have any grasslands which have been abandoned, so our grazing gradient is from lightly grazed to intensively grazed and this probably explains the overall negative effect of grazing on bryophyte richness. Factorial experiments have shown that grazing can also offset negative effects of fertilization on vascular plant diversity to some extent (Borer et al., 2014) and it is plausible that grazing could reduce negative effects of fertilization on bryophytes. However, mowing frequency and grazing intensity are confounded with fertilization in our dataset – because meadows are fertilized with the aim to increase yield and are therefore mown more frequently or grazed more intensively than unfertilized ones – meaning that it is hard to disentangle their effects and not possible to look for interactions between them. However, given the strong negative, direct effects of fertilization on bryophytes it is not likely that increased grazing would be able to completely offset the reduction in bryophyte diversity in fertilized grasslands.

5. Conclusions

Our results challenge the widespread view that the negative effects of fertilization on bryophyte diversity are mostly indirect and mediated by increased light competition with vascular plants. In fact, direct effects, possibly mediated by fertilizer toxicity, can be equally, if not more important. This means that biomass removal alone will not be enough to maintain bryophyte diversity and that reducing fertilizer input is crucial. As bryophyte richness strongly declined with land-use intensification, we recommend keeping fertilizer inputs as low as possible, and reducing mowing frequency and grazing intensity in agricultural grasslands to maintain bryophyte diversity.

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7. References

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Comparing the responses of bryophytes and short-statured vascular plants to climate shifts and

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Table 1: Main geographic and climatic characteristics of the study regions.

Table 2: Summary of linear mixed-effect models separating the effects of the combined fertilization and mowing intensity (LUI Fert/Mow) and the grazing intensity on vascular plant biomass, bryophyte species richness and bryophyte cover in our investigated meadows of the observational dataset. Significant differences are indicated by bold p-values at $P < 0.05$. R^2 denotes the squared correlation coefficient between predicted and observed values.

Figure 1: Structural equation model depicting direct and indirect effects of land-use components on bryophyte species richness. Squares are observed variables. The hexagon is a composite variable. Numbers adjacent to arrows show standardized path coefficients and the width of the line is proportional to the size of the path coefficients. Black lines indicate positive and grey lines negative relationships. Asterisks next to path coefficients indicate p-values ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; n.s. $P < 0.1$. The dashed arrows show co-variances between factors. R^2 denotes the proportion of variance explained for the endogenous variables. Standardized effects (direct times indirect effect) derived from the structural equation models depicted above. **A)** Observational dataset showing the effects of the composite variable land-use intensity – composed by fertilization (F) and mowing (M) intensity – and grazing (G) intensity on plant biomass and bryophyte richness ($X^2 = 0.544$, $P = 0.461$, $df = 1$). **B)** Experimental dataset showing the effect of fertilization and irrigation on plant biomass and bryophyte species richness.