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Low-intensity management promotes bryophyte diversity in grasslands

Extensive Landnutzung fördert die Moosdiversität im Grünland

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Abstract

Bryophytes constitute an important and permanent component of the grassland flora and diversity in Europe. As most bryophyte species are sensitive to habitat change, their diversity is likely to decline following land-use intensification. Most previous studies on bryophyte diversity focused on specific habitats of high bryophyte diversity, such as bogs, montane grasslands, or calcareous dry grasslands. In contrast, mesic grasslands are rarely studied, although they are the most common grassland habitat in Europe. They are secondary vegetation, maintained by agricultural use and thus, are influenced by different forms of land use. We studied bryophyte species richness in three regions in Germany, in 707 plots of 16 m^2 representing different land-use types and environmental conditions. Our study is one of the few to inspect the relationships between bryophyte richness and land use across contrasting regions and using a high number of replicates.

Among the managed grasslands, pastures harboured 2.5 times more bryophyte species than meadows and mown pastures. Similarly, bryophyte cover was about twice as high in fallows and pastures than in meadows and mown pastures. Among the pastures, bryophyte species richness was about three times higher in sheep grazed plots than in the ones grazed by cattle or horses. In general, bryophyte species richness and cover was more than 50% lower in fertilized than in unfertilized plots.

Moreover, the amount of suitable substrates was linked to bryophyte diversity. Species richness of bryophytes growing on stones increased with stone cover, and the one of bryophytes growing on bark and deadwood increased with larger values of woody plant species and deadwood cover.

Our findings highlight the importance of low-intensity land use and high structural heterogeneity for bryophyte conservation. They also caution against an intensification of traditionally managed pastures. In the light of our results, we recommend to maintain low-intensity sheep grazing on sites with low productivity, such as slopes on shallow soils.

Keywords: Biodiversity Exploratories, competition, dry and mesic grasslands, grazing, fertilization, land use, liverwort, meadow, moss, pasture

Erweiterte deutsche Zusammenfassung am Ende des Artikels

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1. Introduction

Semi-natural grasslands are important hotspots of biodiversity in Central Europe for many taxonomic groups, such as vascular plants and insects (WALLISDEVRIES et al. 2002, SILVA et al. 2008, WILSON et al. 2012). At the same time, they belong, together with other grass-dominated systems, to the habitats with the highest rate of decline over the last 100 years (DURAIAPPAH et al. 2005). Two important factors for this habitat loss are the conversion to agricultural land and abandonment of land use (VALKÓ et al. 2018), and apart from that the intensification of land use, which includes fertilization, higher grazing pressures and increased mowing frequencies (POSCHLOD et al. 2005). The effects of different land use and the negative impact of land-use intensification are well documented for the biotic homogenization at the landscape level (GOSSNER et al. 2016), the overall diversity in grasslands (see ALLAN et al. 2014, BOCH et al. 2016a), the diversity of vascular plants (SOCHER et al. 2012, 2013, GILHAUS et al. 2017), lichens (BOCH et al. 2016b) and pollinators (WEINER et al. 2011). However, how these factors influence bryophyte diversity is less well known (e.g., ZECHMEISTER et al. 2003, MÜLLER et al. 2012).

Bryophytes are non-vascular plants comprising mosses, liverworts and hornworts. They reproduce vegetatively via fragments or by producing propagules, such as bulbils, or sexually by gametangia (producing sperms and eggs) after spore germination. These propagules and spores can be dispersed by wind, water or animals (e.g., PORLEY & HODGETTS 2005, BOCH et al. 2015). In general, bryophytes can colonize a wide range of substrates. However, many species are restricted to narrow ecological niches, with specific requirements for substrates and habitat persistence (PORLEY & HODGETTS 2005).

Bryophytes constitute an important and permanent part of the grassland flora (e.g.,WILLEMS 1990, BERGAMINI et al. 2001). They may contribute substantially to the productivity and carbon storage of the vegetation due to their tolerance of extreme conditions such as low nutrient or high moisture levels (TURETSKY 2003, LINDO & GONZALEZ 2010, LINDO et al. 2013). As pioneers, they can rapidly colonize vegetation gaps after disturbances (AUDE & EJRNÆS 2005, PRESTON et al. 2009), where they can facilitate germination (VAN TOOREN 1988, JESCHKE & KIEHL 2008) or effectively compete with seedlings of vascular plants and other bryophytes (KEIZER et al. 1985, RYDIN 1997, DORMANN 2007, SOUDZILOVSKAIA et al. 2011). Finally, the bryosphere is a food resource and, given its high water retention capacity, provides a suitable habitat for other organisms, including many animals (e.g., GERSON 1969, MATERNA 2000, BOCH et al. 2013), symbiotic cyanobacteria (ADAMS & DUGGAN 2008) and other soil organisms (MUELLER et al. 1990, SALMANE & BRUMELIS 2008). Given the pivotal role of bryophytes for the ecological functioning of grassland habitats, it is essential that we understand the drivers of the abundance and diversity of bryophytes.

Because of their narrow ecological niche and sensitivity to habitat change, many bryophyte species are reliable indicators for environmental stressors (HILL et al. 2007, ELLENBERG & LEUSCHNER 2010). How they respond to land-use intensification is poorly explored since most studies on bryophyte diversity and species composition were restricted to specific habitats, such as bogs, montane grasslands, or calcareous dry grasslands (LÖBEL et al. 2006, LOSVIK 2006, PEINTINGER & BERGAMINI 2006, HAWORTH et al. 2007). In contrast, mesic grasslands have been rarely studied, although this type constitutes the majority of grassland habitats in Europe (VIRTANEN et al. 2000, ZECHMEISTER et al. 2003, HEJCMAN et al. 2010). This habitat is under agricultural use and thus, particularly influenced by various

aspects of land use. A comparison of bryophyte diversity and species composition across different land-use types could help us to better understand how this plant group responds to land-use change.

Bryophytes are sensitive to environmental conditions, such as soil properties (e.g., pH), vascular plant cover (LÖBEL et al. 2006) or vascular plant biomass (VAN KLINK et al. 2017) - two factors that are positively related (HEER et al. 2018) – and substrate availability. These variables need to be considered as co-variables when testing land-use effects. Finally, the relative importance of different land-use regimes may depend on the regional setting such as differences in geology and climate. Different regions should therefore be studied to distinguish general trends from those that are more region-specific.

Here, we present the results of a large bryophyte inventory, based on a survey of 707 grassland plots that span different forms of land use. Our aims were: (1) to investigate the impact of land use on bryophyte species richness in grasslands, (2) to identify important environmental conditions that influence bryophyte species richness in addition to land use, (3) to assess whether land-use effects are consistent across regions.

2. Methods

2.1 Study system

The study was conducted as part of the Biodiversity Exploratories program (www.biodiversity-exploratories.de) in grasslands of three regions in Germany (Fig. 1). The first study region, the UNESCO Biosphere Reserve Schorfheide-Chorin, is situated in the young glacial lowlands of North-Eastern Germany, and is characterized by moraines with sandy to loamy soils and fen lowlands with organic fen soil. The second study region, the National Park Hainich and adjacent areas, are located in Central Germany, a region dominated by hills and clay-loamy and calcareous soils. The third study region, the UNESCO Biosphere area Schwäbische Alb (Swabian Jura), is situated in the low mountain ranges of South-Western Germany, which are comprised of gentle hills that are dominated by calcareous soils. While the three study regions differ in climate, geology, and topography (FISCHER et al. 2010; Fig. 1), they harbor similar gradients of land-use regimes and have species pools that are typical for large parts of temperate Europe (BLÜTHGEN et al. 2012).

2.2 Site selection

In each region, we selected 500 grassland sites from the intersection points of a 100 m × 100 m grid (based on the German Gauss–Krüger coordinate system). We discarded study sites fully or partially overlapping with settlements, forests, agricultural fields, and water bodies. We also omitted study sites that were intersected by roads and included only those for which we had the permission to carry out field work. Study sites covered a homogeneously used area of at least 50 m × 50 m (FISCHER et al. 2010). We randomly selected about half of these plots for our study. They covered all possible land-use types in the study regions. This resulted in a total of 707 sites: 141 in the Schwäbische Alb, 296 in the Hainich-Dün, and 270 in the Schorfheide-Chorin area.

2.3 Land-use data

Information on the current land use of every study site was based on questionnaires answered by farmers and land owners. Our plots included temporarily unmanaged fallows (only in Hainich-Dün and Schorfheide-Chorin region), meadows (mown one to four times per year for hay or silage production), pastures grazed by livestock in different densities (sheep, cattle or horses), or mown pastures which were both mown once per year and grazed by livestock in different densities within the same year.

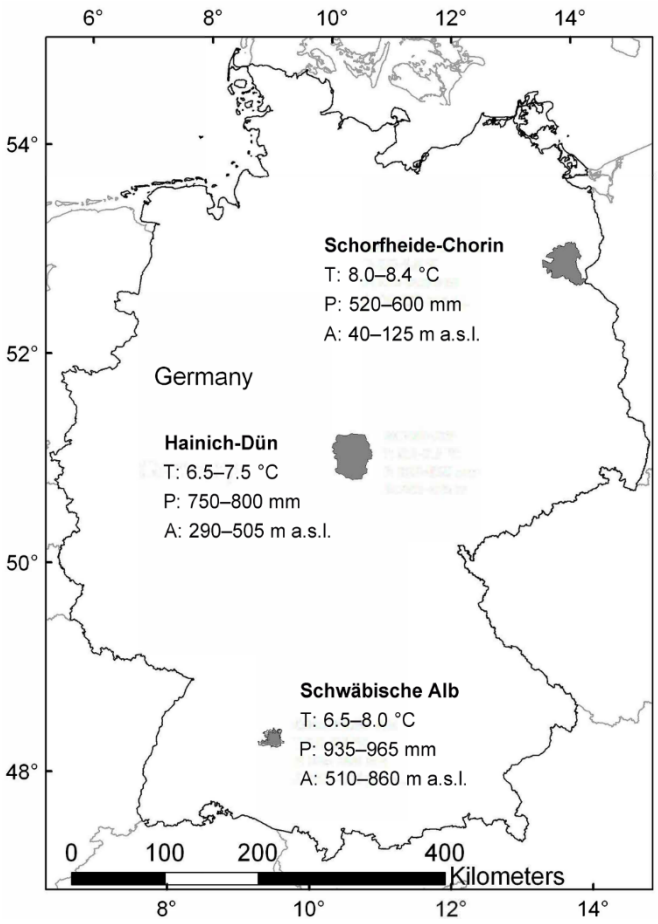


Fig. 1. Location of the three study regions Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb in Germany and the range of mean annual temperature (T), mean annual precipitation (P) and altitude in meters a.s.l. (A) at our study sites. In total, we sampled 707 plots: 270 in the Schorfheide-Chorin, 296 in the Hainich-Dün, and 141 in the Schwäbische Alb area.

Abb. 1. Lage der drei Regionen Schorfheide-Chorin, Hainich-Dün und Schwäbische Alb in Deutschland mit Informationen zur Spanne der durchschnittlichen Jahrestemperatur (T), der durchschnittlichen Jahres-Niederschlagsmenge (P) und der Höhe über dem Meer (A) unserer Untersuchungsflächen. Insgesamt untersuchten wir 707 Grünlandflächen: 270 in der Schorfheide-Chorin, 296 im Hainich-Dün und 141 in der Schwäbischen Alb.

Moreover, grazing regimes differed among livestock types; while sheep-grazed pastures are rotational or grazed by traditional shepherding (minimum of two grazing days per year), pastures grazed by cattle or horses are mainly permanent (up to 240 grazing days per year). For a given time period and area, sheep pastures are thus less intensive than cattle or horse pastures because of less disturbance. Plots were either unfertilized or fertilized to a varying degree. Sheep pastures were generally unfertilized (FISCHER et al. 2010, BLÜTHGEN et al. 2012). They comprised mainly basiphilous meso-xeric dry grasslands (e.g., *Festuco-Brometea* associations), whereas meadows, mown pastures and pastures grazed by cattle or horses were mainly mesophilous to wet grasslands (*Molinio-Arrhenatheretea* associations). The latter often originated from meso-xeric dry grasslands, which have been converted into more intensively managed mesophilous grasslands.

2.4 Vegetation and environmental data

In the summers of 2007 and 2008, we recorded all vascular plant and bryophyte species and estimated their percentage ground cover in 707 plots of 4 m × 4 m. Each plot was located in the center of the 50 m × 50 m study sites. The center of each plot was permanently marked belowground with a metal pole to ensure future relocation. In each plot, we also recorded the presence of species on specific substrate types: soil (terricolous species), stones (saxicolous species), bark and deadwood (corticolous and lignicolous species). This approach allowed us to calculate total and substrate-specific richness values. We also estimated the percentage of the plot area covered by rocks and stones, deadwood and bare soil. In addition, we added up the percentage cover of all vascular plant species in a plot (called cumulative cover henceforth; cumulative cover values can therefore be larger than 100%) to indicate the density of vegetation cover. We identified all bryophytes to the species level except for sterile specimens of *Bryum*, *Pohlia* and *Weissia*, which were only identified to the genus level. Furthermore, we calculated the species richness of acrocarpous and pleurocarpous taxa, respectively. We included liverworts into the pleurocarpous group because of their creeping growth form. Nomenclature of bryophytes follows KOPERSKI et al. (2000).

Close to the center of each plot, the organic layer had been removed with a quadratic 400 cm^2 metal frame. Then the mineral soil was sampled with a motor-driven soil column cylinder (diameter 8.3 cm, length 1m) to obtain undisturbed cores (FISCHER et al. 2010). The soil pH of the uppermost horizon (A, H or E horizon) was determined with a glass electrode in the supernatant of a soil suspension using a 1:2.5 mixture of soil and 0.01 M $CaCl_2$.

2.5 Data analysis

We analyzed the species richness and cover of bryophytes in response to land-use type (fallow, pasture, meadow, mown pasture), livestock type (sheep *vs.* cattle/horse), and fertilization (y/n). As we were analysing count data we chose GLM models with Poisson errors. We used *Chi-square* tests to compare bryophyte richness among our predictors. In cases of overdispersion, quasi-Poisson models were calculated using *F*-tests. Sequential *Chi-square* or *F*-tests were used to test the significance of deviance changes associated with factors added to the model in the sequence shown in Table 1. Differences in bryophyte cover among the factors were tested using linear models. In the analyses, region and co-variates were fitted first. This way, we corrected the effect of land use for regional differences in soil pH, cumulative plant cover and substrate availability. No model selection was performed, but substrate availability was included only for corresponding groups of bryophytes. We did not include interactions between environmental co-variates and region, because environmental effects are expected to be independent of regional differences. Data were analyzed using R, Version 3.3.3 (R CORE TEAM 2017).

3. Results

3.1 Bryophyte species richness

In total we recorded 78 bryophyte taxa in our 707 plots. Overall, we found four times more pleurocarpous than acrocarpous taxa. Most frequent species were *Brachythecium rutabulum* (72.1% of all plots), *Rhytidiadelphus squarrosus* (10.7%), *Calliergonella cuspidata* (9.5%), *Eurhynchium hians* (7.7%), *Barbula unguiculata* (3.9%), and *Physcomitrium pyriforme* (4.4%; only on peat soil). Most of these species have rather broad ecological requirements and occur in various habitats and on different substrates.

Species richness ranged from 0 to 16 species with a low overall average of 2.1 species per plot. Among our study regions, we found pronounced variation in bryophyte richness and cover, with highest values observed in the Schwäbische Alb, intermediate ones in the Hainich-Dün, and lowest in the Schorfheide-Chorin region.

Table 1. Analysis of bryophyte species richness and cover in response to the three study regions, environmental variables, and types of grassland use. Numbers indicate the deviance changes (GLM with Poisson errors) or *F*-values (in italic; GLM with Quasi-Poisson errors and LM in the case of bryophyte cover) for factors (region, land-use type, fertilization, and livestock type), and parameter estimates for continuous variables (soil pH, percentage cover). Significant differences are indicated by bold *p* values.

Tabelle. 1. GLM-Analyse der Moosartenvielfalt und -deckung zwischen den drei Regionen, den Umweltvariablen und den verschiedenen Landnutzungstypen. Gezeigt sind die Abweichungsänderungen (GLM mit Poisson-Fehlern) oder die *F*-Werte (kursiv gedruckt; GLM mit Quasi-Poisson Fehlern und LM im Fall der Moosdeckung) für die Faktoren (Region, Landnutzungstyp, Düngung und Weidetierart) und die Parameter-Schätzungen für die kontinuierlichen Variablen (Boden pH und prozentuale Deckungswerte). Signifikante Unterschiede sind durch fett gedruckte *p*-Werte gekennzeichnet.

		Species richness of all bryophytes		Species richness of bryophytes growing on						Cover of bryophytes (%)	
				Soil		Stones		Bark/deadwood			
Source of variation	*df*	*F*/ Estimates	*p*	*F*/ Estimates	*p*	*Deviance*/ Estimates	*p*	*Deviance*/ Estimates	*p*	*F*/ Estimates	*p*
Region	2	*128.844*	**<0.001**	*109.810*	**<0.001**	*71.820*	**<0.001**	*47.923*	**<0.001**	*50.666*	**<0.001**
Soil pH	1	0.054	**<0.001**	0.057	**0.003**	0.427	**0.004**	0.767	**<0.001**	-2.256	**0.027**
Cumulative vascular plant cover	1	-0.004	**<0.001**	-0.003	**<0.001**	–	–	–	–	-0.100	**<0.001**
Cover bare soil	1	0.007	0.052	0.013	0.058	–	–	–	–	-0.272	**0.016**
Stone cover	1	0.026	**<0.001**	–	–	0.094	**<0.001**	–	–	-0.160	0.284
Woody plant and deadwood cover	1	0.016	**<0.001**	–	–	–	–	0.074	**<0.001**	0.277	**<0.001**
Land-use type	3	*39.688*	**<0.001**	*48.507*	**<0.001**	*28.067*	**<0.001**	*15.274*	**0.002**	*4.240*	**0.006**
Fertilization (yes vs.no)	1	*25.912*	**<0.001**	*30.643*	**<0.001**	*9.456*	**<0.001**	*7.187*	**0.007**	*45.197*	**<0.001**
Livestock type (sheep vs. cattle/horse)	2	*33.022*	**<0.001**	*35.473*	**<0.001**	*0.008*	0.530	*0.660*	0.416	*15.805*	**<0.001**
Region × land-use type	5	*2.088*	0.0651	*1.760*	0.051	*0.345*	0.972	*4.150*	0.528	*2.023*	0.073
Region × fertilization	2	*0.209*	0.8114	*0.183*	0.795	–	–	–	–	*1.209*	0.299
Residual Deviance	≥687	1582.0		1454.7		302.5		353.4		214.1	

3.2 Land-use effects

Land-use intensification strongly reduced bryophyte richness and cover. In Schorfheide-Chorin and Hainich-Dün, fallows harboured more bryophyte species than managed grasslands (pastures, mown pastures, and meadows). Overall, among the managed grasslands, pastures harbored over two and a half times more bryophyte species richness than meadows and mown pastures (Table 2, Fig. 2). Similarly, bryophyte cover was about two times higher in pastures and fallows than in meadows and mown pastures (Tables 1 and 2, Fig. 2).

In general, when we considered only the pastures, we found three times more bryophyte species in sheep grazed plots than in cattle or horse grazed ones (Table 2, Fig. 3).

In general, species richness and cover of bryophytes were positively related (correlation $R^2 = 0.22$, $p < 0.0001$). Bryophyte species richness and cover was more than two times higher in unfertilized than in fertilized plots (2.6 ± 0.1 *vs.* 1.2 ± 0.1 species and 13.1 ± 0.9 *vs.* 4.8 ± 0.6% cover, respectively). In pastures grazed by cattle or horses, bryophyte species richness was two times and cover more than three times higher in unfertilized than in fertilized plots (Tables 1 and 2). This indicates the importance of low-intensity land use for bryophyte conservation.

Table 2. Mean bryophyte species richness and cover in the 4 m × 4 m plots (untransformed mean ±SE) across land-use types and study regions.

Tabelle. 2. Mittelwerte der Moosartenzahlen und -deckungen auf den 4 m × 4 m großen Untersuchungsflächen (untransformierte Mittelwerte ± Standardfehler) für die unterschiedlichen Landnutzungstypen, in den drei Regionen.

Region and land-use- type	*n*	Species richness of all bryophytes	Species richness of bryophytes growing on			Cover of bryophytes (%)
			Soil	Stones	Bark/ deadwood	
Total	707	2.1 (0.1)	2.0 (0.1)	0.1 (<0.1)	0.1 (<0.1)	10.0 (0.6)
Meadow	206	1.2 (0.1)	1.2 (0.1)	0.0 (0.0)	<0.1 (<0.1)	6.2 (0.9)
fertilized	117	1.3 (0.1)	1.3 (0.1)	0.0 (0.0)	0.0 (0.0)	5.0 (1.0)
unfertilized	89	1.1 (0.1)	1.1 (0.1)	0.0 (0.0)	<0.1 (<0.1)	7.8 (1.5)
Mown pasture	189	1.3 (0.1)	1.2 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)	7.8 (1.1)
Sheep	51	1.4 (0.2)	1.3 (0.1)	0.0 (0.0)	0.1 (0.1)	13.5 (3.2)
fertilized	38	1.2 (0.1)	1.2 (0.1)	0.0 (0.0)	0.0 (0.0)	6.2 (1.8)
unfertilized	13	1.9 (0.4)	1.6 (0.3)	0.0 (0.0)	0.4 (0.4)	35.0 (9.5)
cattle/horse	138	1.2 (0.1)	1.2 (0.1)	<0.1 (<0.1)	0.0 (0.0)	5.7 (0.8)
fertilized	86	1.2 (0.1)	1.2 (0.1)	0.0 (0.0)	0.0 (0.0)	4.5 (0.8)
unfertilized	52	1.2 (0.2)	1.1 (0.2)	<0.1 (<0.1)	0.0 (0.0)	7.6 (1.8)
Pasture	270	3.3 (0.2)	3.1 (0.2)	0.1 (<0.1)	0.1 (<0.1)	14.2 (1.2)
sheep unfertilized	142	4.9 (0.3)	4.6 (0.3)	0.2 (0.1)	0.2 (0.1)	21.4 (1.8)
cattle/horse	128	1.5 (0.1)	1.5 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)	6.2 (1.2)
fertilized	21	0.8 (0.1)	0.8 (0.1)	0.0 (0.0)	0.0 (0.0)	2.0 (1.2)
unfertilized	249	1.7 (0.1)	1.6 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)	7.1 (1.4)
Fallow	42	2.5 (0.4)	2.5 (0.4)	0.0 (0.0)	<0.1 (<0.1)	12.3 (2.5)
Schwäbische Alb	141	3.9 (0.3)	3.7 (0.3)	0.2 (0.1)	0.2 (0.1)	20.2 (1.9)
Meadow	42	1.7 (0.2)	1.7 (0.2)	0.0 (0.0)	0.0 (0.0)	11.5 (2.5)
fertilized	37	1.5 (0.1)	1.5 (0.1)	0.0 (0.0)	0.0 (0.0)	10.0 (2.5)
unfertilized	5	3.0 (1.5)	3.0 (1.5)	0.0 (0.0)	0.0 (0.0)	22.7 (9.2)

Region and land-use- type	*n*	Species richness of all bryo-phytes	Species richness of bryophytes growing on			Cover of bryophytes (%)
			Soil	Stones	Bark/ deadwood	
Mown pasture	14	1.2 (0.1)	1.2 (0.1)	0.0 (0.0)	0.0 (0.0)	6.3 (1.9)
sheep	3	1.7 (0.3)	1.7 (0.3)	0.0 (0.0)	0.0 (0.0)	3.5 (2.3)
fertilized	2	2.0 (0.0)	2.0 (0.0)	0.0 (0.0)	0.0 (0.0)	4.3 (3.8)
unfertilized	1	1.0 (0.0)	1.0 (0.0)	0.0 (0.0)	0.0 (0.0)	2.0 (0.0)
cattle/horse fertilized	11	1.1 (0.1)	1.1 (0.1)	0.0 (0.0)	0.0 (0.0)	7.0 (2.3)
Pasture	85	5.5 (0.4)	5.0 (0.4)	0.4 (0.1)	0.3 (0.1)	26.9 (2.7)
sheep unfertilized	76	5.9 (0.5)	5.4 (0.4)	0.4 (0.1)	0.3 (0.2)	26.2 (2.7)
cattle/horse	9	2.1 (0.4)	1.9 (0.3)	0.2 (0.2)	0.0 (0.0)	32.1 (10.5)
fertilized	2	1.5 (0.5)	1.5 (0.5)	0.0 (0.0)	0.0 (0.0)	12.8 (12.3)
unfertilized	7	2.3 (0.5)	2.0 (0.4)	0.3 (0.3)	0.0 (0.0)	37.6 (12.6)
Hainich-Dün	296	2.1 (0.1)	2.0 (0.1)	<0.1 (<0.1)	0.1 (<0.1)	9.8 (0.9)
Meadow	33	1.8 (0.3)	1.8 (0.3)	0.0 (0.0)	0.0 (0.0)	6.2 (1.9)
fertilized	30	1.9 (0.3)	1.9 (0.3)	0.0 (0.0)	0.0 (0.0)	6.2 (2.0)
unfertilized	3	1.0 (0.0)	1.0 (0.0)	0.0 (0.0)	0.0 (0.0)	7.0 (4.2)
Mown pasture	134	1.4 (0.1)	1.4 (0.1)	<0.1 (<0.1)	<0.1 (<0.1)	8.4 (1.3)
sheep	44	1.3 (0.2)	1.2 (0.1)	0.0 (0.0)	0.1 (0.1)	12.1 (3.2)
fertilized	36	1.2 (0.2)	1.2 (0.2)	0.0 (0.0)	0.0 (0.0)	6.3 (1.9)
unfertilized	8	1.9 (0.5)	1.4 (0.3)	0.0 (0.0)	0.6 (0.6)	38.2 (12.1)
cattle/horse	90	1.4 (0.1)	1.4 (0.1)	<0.1 (<0.1)	0.0 (0.0)	6.6 (1.1)
fertilized	68	1.3 (0.1)	1.3 (0.1)	0.0 (0.0)	0.0 (0.0)	4.5 (0.9)
unfertilized	22	1.8 (0.3)	1.7 (0.3)	0.1 (0.1)	0.0 (0.0)	12.8 (3.2)
Pasture	116	2.8 (0.3)	2.7 (0.2)	0.1 (<0.1)	0.1 (<0.1)	11.5 (1.5)
sheep unfertilized	66	3.8 (0.4)	3.6 (0.3)	0.1 (0.1)	0.1 (0.1)	15.7 (2.2)
cattle/horse	50	1.6 (0.2)	1.5 (0.2)	<0.1 (<0.1)	0.1 (<0.1)	5.8 (1.4)
fertilized	12	0.6 (0.1)	0.6 (0.1)	0.0 (0.0)	0.0 (0.0)	0.9 (0.4)
unfertilized	38	1.9 (0.3)	1.8 (0.3)	0.1 (<0.1)	0.1 (0.1)	7.4 (1.8)
Fallow	13	4.0 (0.4)	4.0 (0.4)	0.0 (0.0)	0.2 (0.2)	19.0 (4.1)
Schorfheide-Chorin	270	1.1 (0.1)	1.1 (0.1)	0.0 (0.0)	<0.1 (<0.1)	5.0 (0.7)
Meadow	131	0.9 (0.1)	0.9 (0.1)	0.0 (0.0)	<0.1 (<0.1)	4.5 (1.0)
fertilized	50	0.8 (0.1)	0.8 (0.1)	0.0 (0.0)	0.0 (0.0)	0.5 (0.1)
unfertilized	81	1.0 (0.1)	1.0 (0.1)	0.0 (0.0)	<0.1 (<0.1)	7.0 (1.5)
Mown pasture	41	0.8 (0.2)	0.8 (0.2)	0.0 (0.0)	0.0 (0.0)	6.4 (2.6)
sheep unfertilized	4	2.3 (0.9)	2.3 (0.9)	0.0 (0.0)	0.0 (0.0)	36.8 (19.6)
cattle/horse	37	0.6 (0.1)	0.6 (0.1)	0.0 (0.0)	0.0 (0.0)	3.1 (1.3)
fertilized	7	0.4 (0.2)	0.4 (0.2)	0.0 (0.0)	0.0 (0.0)	0.4 (0.3)
unfertilized	30	0.7 (0.1)	0.7 (0.1)	0.0 (0.0)	0.0 (0.0)	3.7 (1.6)
Pasture	69	1.4 (0.1)	1.4 (0.1)	0.0 (0.0)	0.0 (0.0)	3.2 (1.0)
cattle/horse	69	1.4 (0.1)	1.4 (0.1)	0.0 (0.0)	0.0 (0.0)	3.2 (1.0)
fertilized	7	1.0 (0.2)	1.0 (0.2)	0.0 (0.0)	0.0 (0.0)	0.8 (0.2)
unfertilized	62	1.4 (0.1)	1.4 (0.1)	0.0 (0.0)	0.0 (0.0)	3.4 (1.1)
Fallow	29	1.9 (0.5)	1.9 (0.5)	0.0 (0.0)	0.0 (0.0)	9.3 (3.0)

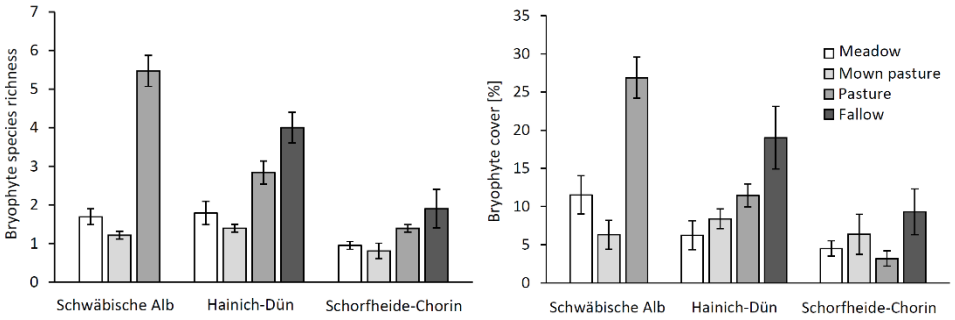


Fig. 2. Mean bryophyte species richness (left) and cover (right) +SE among different land-use types and regions Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin.

Abb. 2. Mittlere Moosartenzahl (links) und -deckung (rechts) mit Standardfehler in den verschiedenen Landnutzungstypen, separat für die Regionen Schwäbische Alb, Hainich-Dün und Schorfheide-Chorin.

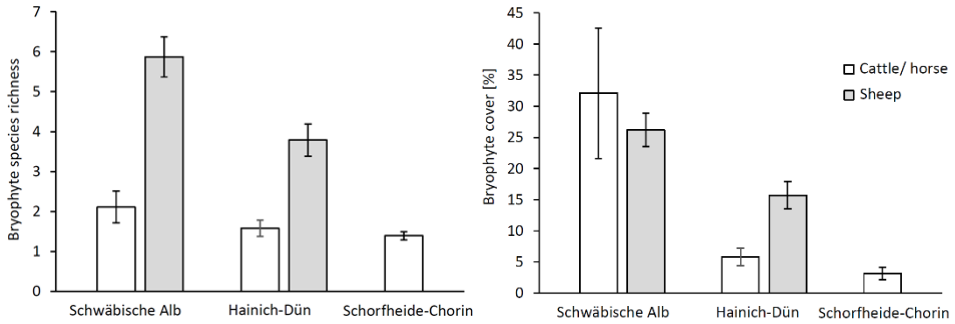


Fig. 3. Mean bryophyte species richness and cover between pastures grazed by cattle/horses and sheep among the regions Schwäbische Alb, Hainich-Dün and Schorfheide-Chorin.

Abb. 3. Mittlere Moosartenzahl (links) und -deckung (rechts) mit Standardfehler in Rinder-/Pferdeweiden und Schafweiden, separat für die Regionen Schwäbische Alb, Hainich-Dün und Schorfheide-Chorin.

3.3 The response of bryophyte species richness to environmental variables

Overall, we found a significant positive relationship between soil pH and bryophyte species richness. In contrast, pH and bryophyte cover were negatively related (Table 1).

Species richness of bryophytes growing on stones increased with increasing cover of stones (Table 1; $R^2 = 0.120$, $p < 0.001$), and the one of bryophytes growing on bark and deadwood increased with larger values of woody plant species and deadwood cover (Table 1; $R^2 = 0.163$, $p < 0.001$). These increased substrate-specific richness values also positively affected total bryophyte species richness per plot (Table 1). This indicates that both the presence and the abundance of a particular substrate is a limiting factor for bryophyte richness and the richness of separate bryophyte groups.

3.4 Relationship between bryophyte and vascular plant species richness and cover

Bryophyte species richness was positively related to vascular plant species richness ($R^2 = 0.469$, $p < 0.001$). However, both bryophyte species richness and cover were negatively related to cumulative vascular plant cover (Table 1; $R^2 = 0.024$, $p < 0.001$ and $R^2 = 0.015$, $p < 0.001$, respectively), suggesting competition between vascular plants and bryophytes.

4. Discussion

4.1 Land-use effects

Our study demonstrated that land use has pronounced effects on bryophyte species richness and composition. These effects remained after we corrected for the effects of environmental variables. Furthermore, we found bryophyte diversity to be positively related to plant diversity. This is consistent with findings of several smaller-scale studies. For example, LÖBEL et al. (2006) observed high bryophyte and vascular species richness in less productive dry grasslands in Öland (Sweden). In a subset of our investigated plots, MANNING et al. (2015) showed that bryophyte diversity is not only related to vascular plant species diversity, but also to the diversities of several invertebrate taxa. In fact, bryophyte diversity showed the strongest relation with the diversity of all other taxa (i.e. multidiversity) at low land-use intensities. This implies that high bryophyte diversity can serve as a proxy for the diversity of many other taxa. However, high land-use intensity substantially weakened these correlations, and bryophytes were the taxon showing the largest decreases in correlation strength between low and high land-use intensities. Thus, land-use intensification could not only lead to a decline of biodiversity but also cause a breakdown of specialized relationships among taxa.

We found negative effects of fertilization on bryophyte species richness. This result is in line with ZECHMEISTER et al. (2003) who studied the effects of land-use practices on bryophytes in 31 plots in Austrian grasslands. Fertilizer application could benefit the growth of competitive vascular plants, increase the competition for light and consequently decrease bryophyte species richness (BERGAMINI & PAULI 2001, AUDE & EJRNÆS 2005, VAN DER WAL et al. 2005, HEJCMAN et al. 2010). Furthermore, high nutrient availability in plots with intense land use can promote nitrophilous bryophyte species (VIRTANEN et al. 2000) and can put bryophyte species that are adapted to poor soil conditions in a competitive disadvantage. This can trigger a change in species composition, including the loss of species with a narrow ecological niche (RYDIN 1997, VAN DER WAL et al. 2005). In particular, large-growing *Brachythecium* species are known to benefit from moderate fertilization (DIRKSE & MARTAKIS 1992), whereas many other less competitive species, e.g., short-statured acrocarpous species suffer from very low amounts of fertilizer. As we only sampled our plot once from early to late summer, it is possible that we even underestimated this effect, because we likely missed some of the annual bryophyte species or the ones fruiting mainly from late autumn to spring (e.g., *Ditrichum cylindricum*, *Leptobryum pyriforme*, *Phascum* spp., *Physcomitriella patens*, *Pottia* spp., *Pterygoneurum ovatum*). These species are confined to microsites with good light conditions and low competition, e.g., open grassland patches, and are therefore more frequently found in grasslands with low-intensity land use (NEBEL & PHILIPPI 2000, 2001).

In addition, fertilization can cause direct toxic effects in plants (e.g., a disturbance of the ionic balance in leaves, which decreases plant longevity and growth: ROELOFS et al. 1985). Bryophytes could be particularly prone to toxic fertilizer effects because they take up water and nutrients through their entire surface rather than through roots and a vascular system. Such toxic fertilizer effects have been identified in experiments with selected moss species (KRUPA 2003, PEARCE et al. 2003, PAULISSEN et al. 2004, ANDERSEN et al. 2016).

Pastures in general, and sheep pasture in particular, revealed highest bryophyte species richness compared to all other managed grasslands. This pattern could be due to several reasons. First, grazing removes biomass and thereby reduces the competition with dominant vascular plants. This in turn leads to higher light availability on the soil surface, which has positive effects for bryophyte species richness. Second, biomass removal by grazers reduces litter accumulation and promotes open patches on the ground. These microsites can be colonized by bryophyte species with a low competitive ability (BOBBINK & WILLEMS 1993, PEINTINGER & BERGAMINI 2006, JASMIN et al. 2008). Third, grazers can suppress competitive vascular plants, create open soil patches and disturb soil through trampling. These disturbances create small gaps in the vegetation, which have been shown to promote bryophyte and vascular plant diversity (BERGAMINI et al. 2001, MÜLLER et al. 2014). The higher richness values in sheep pastures could be explained by more moderate trampling. After all, sheep grazed only for a few days per year at our study sites, whereas cattle and horses grazed permanently. Fourth, biomass removal by grazers can reduce soil-nutrient levels and even compensate for atmospheric N deposition (FOTTNER et al. 2007), and thus benefit bryophyte species richness in pastures. While cattle and horse pastures were either fertilized or unfertilized, sheep pastures were generally not fertilized. SOCHER et al. (2012) showed for a subset of our plots that productivity is higher in cattle and horse grazed pastures than in sheep grazed pastures. This implies that the negative fertilizer effect was largely missing in sheep pastures. Fifth, sheep disperse not only vascular plants (FISCHER et al. 1996) but also bryophyte and lichen fragments (PAULIUK et al. 2011). Compared to permanently fenced cattle and horse grazing regimes, sheep grazing can increase bryophyte diversity by propagule dispersal between grazed sites. In addition, there are indirect positive effects of pastures compared with mown grasslands. In mown grasslands, stones are often removed, woody plant species cut and mole hills and ant nests permanently removed. As a consequence, mowing can homogenize the biological complexity of meadows (MAURER et al. 2006, KLIMEK et al. 2008) by reducing small-scale heterogeneity and diminishing vascular plant (DEAN et al. 1997, MILTON et al. 1997), bryophyte (PRESTON et al. 2009) and lichen species richness (BOCH et al. 2016b).

Another explanation for the low bryophyte species richness in meadows and mown pastures might be the generally high productivity of vascular plants. At the highest values of vascular plant cover, light availability is insufficient to maintain bryophyte viability (VAN DER WAL et al. 2005). This was supported by FESSEL et al. (2016) who found high sward cover and high aboveground biomass to be responsible for low light levels on the ground in German grasslands. Moreover, under intensive land use, bryophytes could fail to colonize vegetation gaps because repeated mowing leads to strong microclimatic changes from shady and moist to sunny and dry, and to alternating periods of desiccation and cessation of growth. Although most bryophyte species are poikilohydric, and therefore generally adapted to such circumstances, such very rapid changes could reduce bryophyte establishment in meadows (VANDERPOORTEN et al. 2003).

Admittedly, the unfertilized sheep-grazed pastures belonged to different vegetation types than the remaining land-use types in our study. Sheep-grazed pastures have either been converted into intensively managed grasslands or are nowadays restricted to sites unsuitable for intensive land use. The latter sites harbor mainly basiphilous meso-xeric dry grasslands (e.g., *Festuco-Brometea* associations), which are known for their high richness of vascular plant, bryophyte and lichen species (DENGLER & BOCH 2008, WILSON et al. 2012). We therefore cannot fully disentangle the effects of the vegetation type from pure management effects on bryophyte species richness. Nevertheless, as we tested and thereby corrected for habitat variables in our models, our results indicate that livestock types itself has an additional effect on bryophyte species richness. An experimental approach could dissect the contribution of these factors in a more powerful manner.

Comparable to sheep grazed pastures, fallows harbored a high bryophyte species richness. Fallows in the Hainich-Dün region were formerly used by the military and were characterized by xeric conditions similar to the studied sheep pastures in this region. Their heterogeneous topography of ditches and groves could have benefitted bryophyte species richness (PRESTON et al. 2009). In contrast, fallows in the Schorfheide-Chorin region were mostly situated on wet fen soils and had low spatial heterogeneity. In both regions, fallows were characterized by high litter accumulation, which has likely reduced their suitability for bryophytes (PEINTINGER & BERGAMINI 2006). In particular, the number of short-living bryophytes was shown to decrease due to litter accumulation (VANDERPOORTEN et al. 2003) and a permanent lack of open soil patches (XIONG & NILSSON 1999). However, in our study, we found no significant relationship between bare soil cover and the richness of bryophyte species. One reason might be that our vegetation sampling in summer may have missed bryophyte species that depend on low-competition conditions and grow mainly from late autumn to spring.

4.2 Environmental variables

Several basic environmental conditions have been shown to affect bryophyte species richness and composition, including climate and microclimate (LONGTON 1982), altitude (BERGAMINI et al. 2001, BRUUN et al. 2006), and atmospheric eutrophication and pollution (BOBBINK et al. 1998). In our study, we found that environmental conditions had a similar effect on bryophyte species richness and cover within regions. This confirms our assumption that although the range of environmental factors differed among regions, the effect of environmental predictors was similar with respects to bryophyte richness and abundance.

Soil conditions are considered to be important determinants of bryophyte species richness and composition (AUSTRHEIM 2001). Our findings support previous studies that found a positive relationship between bryophyte richness and soil pH (e.g., LÖBEL et al. 2006). In addition, soil water availability is important for plant species colonization in grasslands. Particularly wet conditions can hamper typical grassland bryophyte species, leading to reduced species richness on such sites. It is therefore not surprising that the temporarily inundated grasslands of the Schorfheide-Chorin region were characterized by low bryophyte species richness. Their species pool harbored only few bryophyte species that are adapted to changing water levels and the dynamic deposition of sediments and humus after flooding or species that are less specific in their habitat requirements, such as *Calliergonella cuspidata*.

At a small scale, substrate diversity and spatial heterogeneity are considered to be important predictors of bryophyte species richness in grasslands (AUSTRHEIM & OLSSON 1999, LÖBEL et al. 2006, PRESTON et al. 2009). Our study supported this hypothesis by showing

that an increasing cover of stones, woody plants and dead wood facilitates bryophyte richness. These findings indicate that both the presence and the abundance of suitable substrates plays an important role for promoting bryophyte diversity.

The presence of bare soil is considered to be important for the colonization of several small bryophyte species. In line with ZECHMEISTER et al. (2003), we found that bare soil had a positive effects. In our study particularly acrocarpous species, such as *Bryum* spp. and *Barbula* spp., which are considered as pioneer species of low competitive abilities (NEBEL & PHILIPPI 2000, 2001), profited from bare soil.

5. Conclusions

Our study demonstrated that an intensive use of grasslands, encompassing high levels of fertilization and mowing, is linked to low bryophyte species richness. It is also associated with a different bryophyte species composition, dominated by few nitrophilous species with mostly unspecific ecological requirements. Given its strong sensitivity, bryophyte diversity can be a suitable indicator for land-use change. Furthermore, at low land-use intensities, bryophyte richness can be used as a proxy for the diversity of many other taxa in grasslands (MANNING et al. 2015). By including bryophytes as study organisms, future studies in grassland ecology could help us to better understand the effects of different land use on our environment.

Our findings highlight the importance of low-intensity land use and high structural heterogeneity for bryophyte conservation. Environmental policy and management should therefore avoid intensifying existing pastures that are traditionally managed and unfertilized. Moderate degrees of sheep grazing (e.g., migratory shepherding) on sites of low productivity, such as slopes on shallow soils, are particularly valuable for bryophyte conservation.

Erweiterte deutsche Zusammenfassung

Einleitung – Halbnatürliche, extensiv bewirtschaftete Grünländer sind Biodiversitätshotspots Mitteleuropas (WILSON et al. 2012). Moose sind ein wichtiger Bestandteil dieser Biodiversität. Aufgrund der spezifischen Ansprüche und der Empfindlichkeit vieler Moosarten gegenüber Umweltveränderungen ist ein Rückgang der Moosdiversität durch intensive Landnutzungsformen zu erwarten. Während sich Untersuchungen zur Moosdiversität bislang hauptsächlich auf Offenlandhabitate mit hoher Moosdiversität beschränkten (z. B. Trockenrasen, Moore; LÖBEL et al. 2006, PEINTINGER & BERGAMINI 2006), fand mesophiles oder intensiv genutztes Grünland, also der Großteil der mitteleuropäischen Kulturlandschaft, bislang kaum Beachtung. Neben der Landnutzung spielen verschiedene Umweltparameter eine wichtige Rolle zur Erklärung von Diversitätsmustern bei Moosen (z. B. pH-Wert des Bodens, Vegetationsdeckung; LÖBEL et al. 2006) und sollten deshalb in Analysen einbezogen werden.

Im Rahmen dieser Studie untersuchten wir deshalb die Diversität von Moosen in unterschiedlichen Grünlandtypen mit unterschiedlichen Nutzungsregimen. Wir untersuchten zudem welche Umweltparameter neben den Landnutzungseffekten die Muster der Moosdiversität erklären. Um generelle Trends von regionalen zu unterscheiden, führten wir unsere Untersuchungen in drei verschiedenen Regionen durch.

Methoden – Wir untersuchten 707 unterschiedlich bewirtschaftete Grünlandflächen, im Rahmen des von der Deutschen Forschungsgemeinschaft geförderten Forschungsprogramms „Biodiversitäts-Exploratorien“. Die Untersuchungen fanden in drei Regionen statt, dem (1) Biosphären Reservat Schorfheide-Chorin, (2) dem Nationalpark Hainich und der diesen umgebenden Hainich-Dün-Region und (3) dem Biosphärengebiet Schwäbische Alb. Diese Regionen decken den Nord-Süd-Gradienten Deutschlands in Klima, Geologie und Topografie ab. In allen Regionen gibt es eine große Vielfalt von

extensiv bis relativ intensiv genutztem Grünland. Informationen zur Landnutzung basieren auf Befragungen der Bewirtschafter. Unsere Untersuchungsflächen umfassten vier unterschiedliche Landnutzungsformen: temporär ungenutzte Brachen, Wiesen (ein- bis viermal gemäht), Weiden (Schafe, Rinder/Pferde) und Mähweiden (beweidet und zusätzlich einmal pro Jahr gemäht). Die Flächen waren zudem entweder gedüngt oder ungedüngt. Die Untersuchungsflächen waren zudem auf einer Fläche von mindestens 50 m × 50 m homogen bewirtschaftet (Details siehe FISCHER et al. 2010, BLÜTHGEN et al. 2012).

Im Zentrum dieser Untersuchungsflächen nahmen wir alle Gefäßpflanzen- und Moosarten in einen 4 m × 4 m großen, permanent unterirdisch markierten Quadrat auf und schätzten ihre prozentualen Deckungen. Die Moose erfassten wir zudem getrennt nach Substraten (Boden, Stein, Rinde und Totholz) und schätzten die prozentualen Deckungen der Substrate. Wir addierten anschließend die Deckungsgrade aller in einer Untersuchungsfläche vorkommenden Gefäßpflanzenarten („cumulative cover"), um eine Aussage über die Vegetationsdichte machen zu können. Im Zentrum jeder Fläche wurde eine Bodenprobe genommen und der pH-Wert des obersten Horizontes gemessen.

Wir analysierten, wie sich die Moosartenvielfalt und -deckung zwischen den vier Landnutzungstypen, den Weidetierarten (Schafe *versus* Rinder/Pferde) und gedüngten und ungedüngten Flächen unterscheidet, nachdem wir für Region und die Co-Variablen (pH-Wert, Überdeckungsgrad der Vegetation, Substratverfügbarkeit) korrigierten. Wir verwendeten dafür Generalisierte Lineare Modelle (GLM) und im Fall der Moosdeckung Lineare Modelle (LM; Sequenz s. Tab. 1).

Ergebnisse – Temporär ungenutzte Brachen, die nur in der Schorfheide-Chorin und dem Hainich-Dün vorkamen, beherbergten mehr Moosarten als die genutzten Grünländer in den beiden Regionen. Was das genutzte Grünland betrifft, so kamen in Weiden 2,5 mal mehr Moosarten vor als in Wiesen und Mähweiden. In Brachen und Weiden war zudem die von Moosen bedeckte Fläche doppelt so groß wie jene in Wiesen und Mähweiden (Tab. 1 und 2, Abb. 2). Schafweiden wiesen eine dreimal höhere Moosartenvielfalt als Rinder- oder Pferdeweiden auf (Tab. 2, Abb. 3). Düngung halbierte die Moosartenvielfalt und -deckung (Tab. 1 und 2).

Der pH-Wert des Bodens und die Moosartenvielfalt waren positiv korreliert. Je höher die Deckung eines Substrates, desto mehr Moosarten waren auf dem jeweiligen Substrat zu finden (Tab. 1).

Diskussion – Unser Ergebnis eines negativen Düngereffektes auf die Vielfalt von Moosen bestätigt die Berichte anderer Studien aus verschiedenen Grünlandtypen. Dies ist zum einen auf das geförderte Wachstum von Gefäßpflanzen zurückzuführen, wodurch viele konkurrenzschwache Moosarten verdrängt werden (z. B. ZECHMEISTER et al. 2003). Zum anderen können toxische Düngereffekte dafür verantwortlich gemacht werden (KRUPA 2003, PEARCE et al. 2003, PAULISSEN et al. 2004).

Wir fanden eine höhere Artenzahl von Moosen in temporär ungenutzten Brachen als im genutzten Grünland. Dieses Ergebnis könnte damit zusammenhängen, dass einige Brachen eine höhere kleinräumige Heterogenität mit zahlreichen geeigneten Substraten und Mikrohabitaten aufweisen (PRESTON et al. 2009).

Wir konnten außerdem zeigen, dass Weiden, in unserem Fall besonders die extensiv genutzten Schafweiden, generell mehr Moosarten beherbergen als gemähtes Grünland. Dieser positive Beweidungseffekt ist wahrscheinlich eine Kombination verschiedener Faktoren. Die Entnahme von Biomasse kann die Konkurrenz zwischen Moosen und Gefäßpflanzen reduzieren und die Streuakkumulation verhindern, wodurch Bodenmoose gefördert werden (BOBBINK & WILLEMS 1993, PEINTINGER & BERGAMINI 2006, JASMIN et al. 2008). Kombiniert mit moderaten Störungen (z. B. durch Vertritt), können offene Stellen entstehen, die von konkurrenzschwachen Moosen besiedelt werden können (BERGAMINI et al. 2001, MÜLLER et al. 2014). Außerdem ist die kleinräumige Heterogenität in gemähten Wiesen generell geringer als in Weiden, da Steine und Büsche entfernt und somit potentielle Wuchsorte zahlreicher Moosarten dezimiert werden (vgl. PRESTON et al. 2009). Unser Ergebnis, dass nicht nur die Anwesenheit, sondern auch die Menge eines geeigneten Substrates wichtig zur Erklärung der Moosartenvielfalt ist, unterstreicht diesen Effekt.

Die höheren Moosartenzahlen in Schafweiden als in Rinder- oder Pferdeweiden könnten darauf zurückzuführen sein, dass unsere untersuchten Schafweiden nur wenige Tage pro Jahr beweidet und generell ungedüngt waren. Auf den zur Vegetationszeit meist permanent bestellten Rinder- und Pferdeweiden könnte zum einen die mechanische Störung zu hoch für einige Moosarten sein, zum anderen könnte hier der erhöhte Düngereintrag negativ wirken.

Bodenparameter können die Moosdiversität und Artenzusammensetzung beeinflussen (AUSTRHEIM 2001). Die positive Beziehung zwischen Moosartenvielfalt und pH-Wert des Bodens wurde bereits in zahlreichen Studien gezeigt (z.B. LÖBEL et al. 2006). Bodenparameter sollten deshalb neben der Landnutzung in zukünftigen Studien zu Diversitätsmustern von Moosen im Grünland berücksichtigt werden.

Schlussfolgerungen – Unsere Ergebnisse legen nahe, dass extensive Bewirtschaftungsmethoden, wie der Verzicht auf Dünger und die Beweidung mit geringen Bestockungsdichten, sowie die Förderung der kleinräumigen Heterogenität wichtig für den Erhalt der Moosartenvielfalt im Grünland sind. Die Intensivierung von Grünland sollte deshalb gestoppt und die extensive Bewirtschaftungsweise durch gezielte Agrarumweltprogramme gefördert werden.

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