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Quick recovery of bryophyte species richness but not cover after sward disturbance along a land-use intensity gradient in grasslands

Schnelle Erholung der Moosartenvielfalt, jedoch nicht der Moosdeckung nach Bodenstörung in Grasländern entlang eines Gradienten der Landnutzungsintensität

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Abstract

In semi-natural grasslands, land-use intensification is considered as one of the major drivers of habitat degradation, leading to biodiversity decline. The recovery of biodiversity and ecosystem functions in grasslands after disturbances, i.e. the ability to return to previous conditions, is of particular importance from an economical but also a conservational point of view, as ecosystem functions ensure the provision of ecosystem services. Accordingly, sowing of seed mixtures is widely used to restore grasslands, often combined with sward disturbances to increase the establishment success. However, while sward disturbances initially affect vascular plants drastically, the effects on the bryophytes are largely unclear. Moreover, it is unclear whether seed addition affects bryophyte recovery and species richness and whether land-use intensity interacts with the recovery of bryophyte communities after disturbances. To test the effects of disturbance, separately and in combination with seeding, along a gradient in land-use intensity on bryophyte communities, we established a full factorial experiment with each four 7 m × 7 m treatment subplots (control, seeding only, seeding and disturbance, disturbance only) in 72 agricultural grasslands in Germany. In 2 m × 2 m quadrats per treatment subplot, we monitored the recovery of bryophyte communities over two years. Disturbances strongly decreased bryophyte richness and cover and led to a high Sørensen dissimilarity between disturbed and undisturbed subplots. While richness and cover in general strongly decreased with increasing land-use intensity, the decrease in richness due to disturbance was strongest at low land-use intensity, where bryophyte richness was generally higher. In the second year of the experiment, species richness did not differ anymore between disturbed and undisturbed subplots, and species composition became more similar between disturbed and undisturbed subplots, indicating a recovery of the communities. However, bryophyte cover did not recover. Interestingly, land-use intensity and seeding in general had no significant effect on the recovery of bryophyte species richness and cover. The quick recovery of

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bryophyte species richness indicates that grassland-restoration measures including disturbances and seed addition seem to have no detrimental effects on bryophyte diversity. However, ecosystem functions provided by bryophytes might be limited until bryophyte cover is fully restored.

Keywords: bryophyte, colonization, community recovery, disturbance experiment, Germany, land-use intensity, seed addition, semi-natural grassland, species richness, vegetation cover

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Grasslands are highly diverse ecosystems, harbouring many specialized species (Dengler et al. 2020, Biurrun et al. 2021) and providing important ecosystem functions and services such as biomass production, carbon fixation and erosion prevention (Rounsevell et al. 2018). They are also spatially relevant since about 20% of the territory of the Palaearctic biogeographic realm and about 15% of temperate (Western) Europe are covered by grasslands (Boch et al. 2020, Dengler et al. 2020). Bryophytes are often a relevant component of species diversity in grasslands, where they often form a closed understory layer below the vascular plants (Boch et al. 2018b, Biurrun et al. 2021). Moreover, bryophyte richness may serve as an indicator for the diversities of other plant and animal taxa as well as for overall species diversity (Manning et al. 2015, Boch et al. 2021). In addition, bryophytes importantly contribute to ecosystem functions such as water and microclimate regulation and nutrient cycling (Turetsky 2003, Jaroszynska et al. 2023, Slate et al. 2024).

Today, many semi-natural grassland types are among the most endangered habitats and have strongly declined in extent, quality and biodiversity during the past decades (Janssen et al. 2016, Rounsevell et al. 2018). In Western Europe, land-use changes including intensification and the abandonment of traditional land-use systems, as well as the conversion of grasslands to built-up areas and arable fields (e.g. for biogas production), are considered as major drivers of grassland habitat destruction and degradation (Rounsevell et al. 2018, Boch et al. 2020). Land-use intensification comprises the application of large amounts of fertilizer with the aim to increase yields, often in combination with increased mowing frequencies and grazing at higher stocking densities (Blüthgen et al. 2012). This results in long-term declines of species richness and changes in species composition of plants and other taxa (Allan et al. 2014, Gossner et al. 2016). Likewise, grassland bryophyte richness is also declining with increasing land-use intensity (Boch et al. 2018a, Virtanen et al. 2025). On the one hand, this decline can be attributed to an indirect negative effect of fertilization, leading to an increase of vascular plant biomass and competition for light (Carroll et al. 2000, Bergamini & Pauli 2001, Boch et al. 2018b). On the other hand, fertilization can have a direct negative effect on bryophyte richness and cover via toxic fertilization effects (Carroll et al. 2000, Andersen et al. 2016, Lin et al. 2025) that might be even stronger than the indirect effect mediated by increased vascular plant biomass (Boch et al. 2018a, Lin et al. 2025).

The recovery of biodiversity and ecosystem functions in agricultural grasslands after disturbances, i.e. the ability to return to previous conditions, is of particular importance from an economical but also a conservational point of view, as ecosystem functions ensure the provision of ecosystem services (Allan et al. 2015, Schäfer et al. 2019). A high species richness of multiple taxa across trophic levels has been shown to be a key feature to maintain ecosystem functions (Soliveres et al. 2016). Moreover, species-rich ecosystems have been suggested to be more stable (McCann 2000, Blüthgen et al. 2016) and to recover faster – in terms of ecosystem functions – after disturbances than species-poor ones, as the chance of

containing redundant species substituting a specific function after disturbance is increasing with a high number of species in a community (insurance hypothesis Yachi & Loreau 1999). Thus, restoring grassland habitats and their biodiversity to maintain and improve ecosystem functions are a major target of the EU Biodiversity Strategy (Hermoso et al. 2022).

Sowing of seed mixtures or hay transfer are among the most widely used methods to restore grasslands, i.e. to increase plant species richness in degraded grasslands or former arable fields (Kiehl et al. 2010, Klaus et al. 2017, Sommer et al. 2025). These seed-addition methods are often necessary to complement the spontaneous dispersal and colonization process of plant species in fragmented landscapes, especially of dispersal limited species (Stein et al. 2008, Török et al. 2018). However, seed germination and establishment are strongly limited in permanent grasslands with a closed sward because they lack open patches for germination and due to competition for light by established plants (Kiehl et al. 2010). Thus, seed addition is often combined with sward disturbances to overcome these limitations and to activate the soil seedbank (Bossuyt & Honnay 2008, Klaus et al. 2017). Strong sward disturbances initially affect vascular plants drastically, but the effects on the bryophyte layer are largely unclear. As most bryophytes establish in open patches with reduced light competition by vascular plants, bryophyte richness and cover might even profit from sward disturbances (Zechmeister & Moser 2001). However, only few studies included bryophytes when studying disturbance effects on plant species richness, thus the recovery of bryophyte communities after drastic disturbances is largely unexplored (but see Chytrý et al. 2001, Hydbom et al. 2012, Müller et al. 2014). In addition, it is largely unknown whether increased species richness of vascular plants by seed addition affects the recovery and species richness of bryophytes (but see Lin et al. 2025). Finally, it has not been tested yet whether land-use intensity interacts with the recovery of bryophyte communities after disturbances, although it is likely that land-use intensity interacts with sward disturbance while affecting bryophytes. Insight into these effects will help to understand how bryophyte diversity is affected by grassland restoration that involves sward disturbance.

The aim of this study was to determine the effects of disturbance, separately and in combination with vascular plant seed addition, along a gradient in land-use intensity on bryophyte species richness and cover in agricultural grasslands. We monitored the recovery of bryophyte communities over two years after disturbance in 72 permanent grasslands in Germany. We define recovery as the ability of bryophyte species richness and cover to return to conditions before disturbances were applied.

Our main questions were: (1) How is bryophyte species richness and cover affected by sward disturbances and seed addition of vascular plants, separately and in combination? (2) Do bryophyte species richness and cover recover in the short-term, i.e., within one year after sward disturbance, and is recovery affected by seed addition? (3) Are the disturbance effect and the recovery of bryophytes affected by the previous land-use intensity of the grasslands?

2. Methods

2.1 Study sites

The study was conducted as part of the Biodiversity Exploratories program (www.biodiversity-exploratories.de; Fischer et al. 2010) in 72 agricultural grasslands of three regions in Germany: (i) The UNESCO Biosphere Reserve Schorfheide-Chorin, is situated in North-Eastern Germany (53.0°N, 14.0°E). It comprises young glacial lowlands and is characterized by moraines with sandy to loamy

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

Tabelle 1. Geografische und klimatische Eigenschaften der Untersuchungsgebiete.

Region	Schwäbische Alb	Hainich-Dün	Schorfheide-Chorin
Location	SW Germany	Central Germany	NE Germany
Elevation a.s.l.	460–860 m	285–550 m	3–140 m
Mean annual temperature	6.0–7.0 °C	6.5–8.0 °C	8.0–8.5 °C
Mean annual precipitation	700–1000 mm	500–800 mm	500–600 mm

soils as well as organic fen soils. (ii) The National Park Hainich and surrounding areas are located in Central Germany (51.1°N, 10.4°E), predominantly having clayish to loamy soils over calcareous bedrock. (iii) The UNESCO Biosphere area Schwäbische Alb (Swabian Jura) is situated in the mountain ranges of South-Western Germany (48.4°N, 9.4°E), which are composed of calcareous bedrock. The three study regions cover a gradient of precipitation (decreasing from SW to NE), annual mean temperature (increasing from SW to NE) and elevation a.s.l. (decreasing from SW to NE; Table 1). Yet, the regions harbour similar gradients of land-use regimes and land-use intensities, which are typical of large parts of temperate Europe (Blüthgen et al. 2012).

2.2 Land-use data

For this study, 72 grasslands were selected that strongly differed in vascular plant and bryophyte species richness as well as in land-use intensity (Socher et al. 2012, Klaus et al. 2017, Boch et al. 2018a). To be able to compare the different management types of the grasslands, we gathered information on land-use intensity via questionnaires with farmers and landowners. The grasslands were managed either as meadows (mown one to four times per year for hay or silage production), pastures (grazed by sheep, cattle or horses at different densities), or so-called mown pastures, which were regularly mown and grazed by livestock. In addition, grasslands were either unfertilized or fertilized to different extents (Blüthgen et al. 2012). We quantified land-use intensity (LUI) for each plot according to Blüthgen et al. (2012) using an integrated LUI measure, which sums up the standardized intensities of fertilization (kg nitrogen × ha-1 × y-1), the frequency of mowing (number of cuts × y-1) and the grazing intensity (number of livestock units × grazing days × ha-1 × y-1) for each grassland in 2015 and 2016 (for details and examples how different land-use intensity scenarios are quantified see Boch et al. 2018a). Land-use intensity was calculated as global mean of grassland management using the LUI calculation tool (Ostrowski et al. 2020) implemented in BExIS (http://doi.org/10.17616/R32P9Q).

2.3 Experimental design

In each of the 72 agricultural grasslands (25 in the Schwäbische Alb, 23 in Hainich-Dün, 24 in Schorfheide Chorin), we established a full-factorial experiment with seeding and sward disturbance in four 7 m × 7 m treatment subplots (control, seeding only, seeding and disturbance, disturbance only) per site. Subplots were separated by 2 m buffers (Fig. 1). In October 2014, the disturbance treatment was applied by mechanical perturbation (rotary harrowing) of the topsoil (to approx. 10 cm depth) using a rotary harrow, a method that creates a high proportion of bare ground (on average around 50% in the following spring; Schäfer et al. 2019). This technique is commonly used in re-seeding practices (Sommer et al. 2025). Bryophyte and vascular plant (root and shoot) fragments of the disturbed sward were not removed but left on the ground, allowing regrowth (Fig. 2; see Klaus et al. 2017 for further details on the experimental design and treatments).

For the seeding treatments, we used specific mixtures of locally produced seeds of native plant species for each of the three regions. Seed mixture composition was determined according to local species pools (derived from vegetation records by Socher et al. 2012 and Klaus et al. 2013) and availability of regional seeds at certified seed producers. Mixtures consisted of common and less-common grass, legume and forb species that naturally occur in the respective region. For further details on the species sown in the three regions, see Klaus et al. (2017).

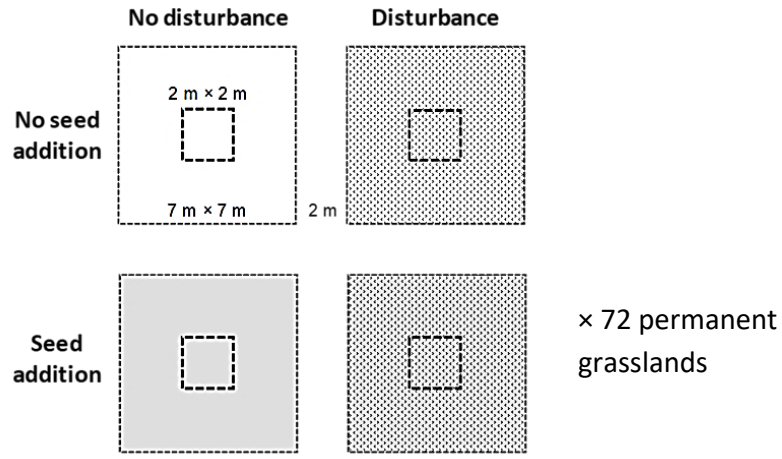

Fig. 1. Design of the full-factorial experiment combining disturbance and high-diversity seed addition including their combination and a control subplot, each with a central 2 m × 2 m monitoring quadrat for the bryophyte sampling. Note that in some cases subplots may have been placed in other arrangements (modified according to Klaus et al. 2017).

Abb. 1. Skizze des vollfaktoriellen Experiments, das Störungen und die Zugabe von Saatgut mit hoher Vielfalt kombiniert, einschließlich ihrer Kombination und einer Kontroll-Teilfläche, jeweils mit einem zentralen 2 m × 2 m großen Untersuchungsfläche für die Moosaufnahme. In einigen Fällen wurden die Teilflächen anders angeordnet (modifiziert nach Klaus et al. 2017).

Fig. 2. After the disturbance with a rotary harrow, on average around 50% of bare ground remained in the following spring. Bryophyte and vascular plant (root and shoot) fragments of the disturbed sward were not removed but left on the ground, allowing regrowth (Photo: V. Klaus, 2015).

Abb. 2. Nach der Bodenbearbeitung mit einer Kreiselegge blieben im folgenden Frühjahr durchschnittlich etwa 50 % des Bodens unbedeckt. Fragmente von Moosen und Gefäßpflanzen (Wurzeln und Triebe) der bearbeiteten Grasnarbe wurden nicht entfernt, sondern auf dem Boden belassen, sodass sie wieder nachwachsen konnten (Foto: V. Klaus, 2015).

2.4 Field surveys and data preparation

In the centre of all treatment subplots, we established a 2 m × 2 m monitoring quadrat (Fig. 1), in which we recorded all bryophyte species and their percentage cover. In Hainich-Dün and the Schwäbische Alb, we conducted bryophyte surveys in May and June 2015 and 2016 and in the Schorfheide-Chorin region in September 2015 and 2016. Species that could not be identified in the field were collected and identified later in the lab. Nomenclature of bryophytes follows Koperski et al. (2000).

We then calculated total species numbers and cumulative cover (summing up the cover of the individual species) of bryophytes for each monitoring subplot. We further grouped bryophyte species according to their life history strategy in short-lived (r strategists) and long-lived species (k strategists) based on Van Zuijlen et al. (2023).

2.5 Statistical analysis

Data were analyzed using R, Version 4.3.1 (R Core Team 2023). We used linear mixed effect models and generalized linear mixed effect models (package lme4; Bates et al. 2015) to test for treatment and land-use intensity effects on species richness and cover of bryophytes, in 2015 and 2016. We fitted GLMM models with a Poisson distribution to estimate species richness, and with a binomial distribution (logit link) for species cover. We treated grassland identity (72 levels) nested in region (3 levels) as random factors to correct for region specific differences and account for the subplots being nested within grassland sites. We included the single treatments (disturbance and seed addition) and their interaction (disturbance × seeding) as well as land-use intensity as fixed factors. To test whether the treatment effects differed along the land-use intensity gradient, we fitted an interaction between treatment and land-use intensity. Full models were simplified by dropping terms that did not significantly improve the overall model fit using likelihood ratios (Zuur et al. 2009).

We calculated the turnover of taxa between each disturbed and undisturbed subplot using Sørensen dissimilarity (Sørensen 1948): turnover = $b+c/(2a+b+c)$, where b is the number of taxa present in the disturbed but not undisturbed subplots, c is the number of taxa present in the undisturbed but not disturbed subplots, and a is the number of taxa shared by both. We then fitted a lmer model with region as a random term (p-values calculated using the package lmerTest; Kuznetsova et al. 2017).

For all models, we calculated R^2m as the marginal coefficient (proportion of variance explained by fixed factors alone) and R^2c as the conditional coefficient (proportion of variance explained by both, fixed and random factors) of determination for all mixed-effect models (Nakagawa & Schielzeth 2013; MuMin package: Barton 2018, Tables 2 and 3). Our data met the model assumptions of homogeneity of variance and normal distribution of residuals.

3. Results

Over two years and across all 288 subplots, we recorded in total 52 bryophyte taxa (excluding uncertain identifications). The number of taxa per subplot ranged from 0 to 15, with an average of 2.7 (± 2.3 SD) in 2015 and 4.0 (± 2.8 SD) in 2016. The most frequent species were *Brachythecium rutabulum* (occurred in 82% of all subplots), *Eurhynchium hians* (38%) and *Plagiomnium affine* (22%). Richness and cover of bryophytes were generally higher in low than in high land-use intensity sites (Fig. 3). Moreover, the community composition differed along the land-use intensity gradient, with a tendency of more short-lives species (r strategists) in plots with high land-use intensity (Supplement E1).

3.1 Effect of disturbance and seed addition along the land-use intensity gradient

In 2015, disturbance decreased bryophyte richness from 3.4 to 2.0 species (Fig. 3a, Table 2), and bryophyte cover from 25 to 4% on average (Fig. 3b, Table 2). Disturbance further led to a high Sørensen dissimilarity between all disturbed and all undisturbed

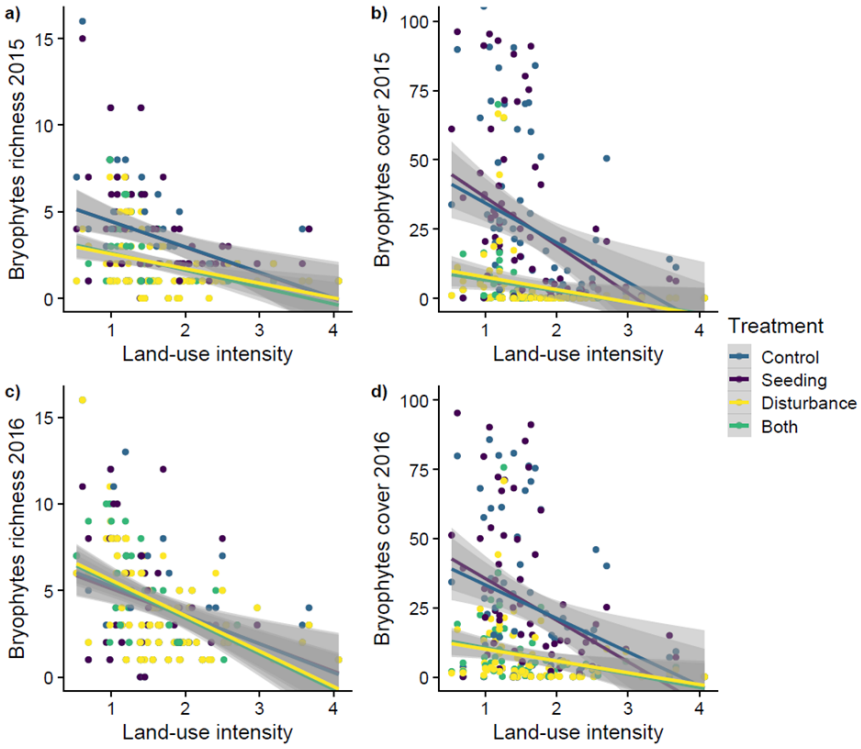

Fig. 3. Effect of the seeding and disturbance treatments on (a, c) species number and (b, d) cover (in %) of bryophytes across the land-use intensity gradient, (a, b) in 2015 and (c, d) in 2016. Gray-shaded areas around the regression lines show standard errors (displayed are simple lm regression lines and standard errors).

Abb. 3. Auswirkung der Ansaat- und Störungsmaßnahmen auf (a, c) die Artenzahl und (b, d) die Deckung (in %) von Moosen über den Landnutzungsintensitätsgradienten hinweg, (a, b) im Jahr 2015 und (c, d) im Jahr 2016. Die grau schattierten Bereiche um die Regressionslinien zeigen Standardfehler (angezeigt werden einfache Regressionslinien des linearen Modells und Standardfehler).

subplots (Fig. 4, Table 3) indicating changes of the community composition (Supplement E2). Richness and cover strongly decreased with increasing land-use intensity (Table 2). The decrease in richness due to disturbance was strongest at low land-use intensity, where bryophyte richness was generally higher. Yet, bryophyte richness remained higher in disturbed low land-use intensity subplots than in both disturbed and undisturbed high land-use intensity subplots (Fig. 3a). Seed addition had no significant influence on bryophyte richness and cover (Table 2).

3.2 Recovery of the communities along the land-use intensity gradient

In 2016, species richness did not differ significantly between disturbed and undisturbed subplots anymore (Fig. 3c, Table 2). In addition, species composition became more similar between disturbed and undisturbed subplots (i.e., low dissimilarity shown in Fig. 4, Table 3), indicating a recovery of the communities also in terms of species identity (mean ± SE difference in Sørensen values between disturbed and undisturbed plots in 2015: 0.39 ± 0.02;

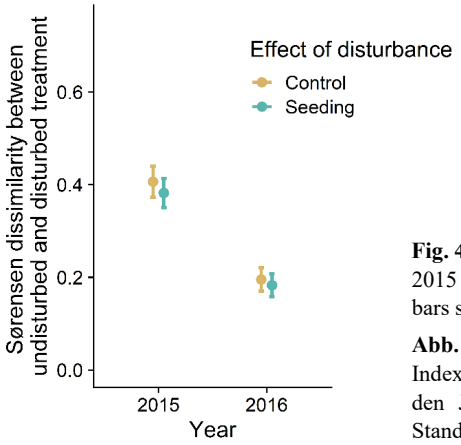

Fig. 4. Effect of disturbance on the Sørensen index in 2015 and 2016 in unseeded and seeded subplots. Error bars show standard errors.

Abb. 4. Auswirkung von Störungen auf den Sørensen-Index auf eingesäten und nicht eingesäten Teilflächen in den Jahren 2015 und 2016. Die Fehlerbalken zeigen Standardfehler.

in 2016: 0.19 ± 0.02). However, bryophyte cover did not recover from 2015 to 2016 (Fig. 3d, Table 2). Land-use intensity and seeding in general had no significant effect on the recovery of bryophyte species richness and cover (non-significant disturbance × seed addition and disturbance × LUI interactions in 2016; Table 2).

Table 2. Results of the generalized mixed effects models estimating the effect of treatments and land-use intensity (LUI) and their interactions on the number of species (Poisson model) and on the cumulative cover of bryophytes (binomial model), in 2015 and 2016. Full models were simplified by dropping terms that did not significantly improve the overall model fit using likelihood ratios (removed terms are displayed in grey). Estimates were calculated for the reduced models. All models included grassland identity nested in region as a random term. R^2m was calculated as the marginal coefficient (proportion of variance explained by fixed factors alone) and R^2c as the conditional coefficient (proportion of variance explained by both, fixed and random factors) of determination for all mixed-effect models.

Tabelle 2. Ergebnisse der verallgemeinerten gemischten Effektmodelle zur Schätzung der Auswirkungen von Behandlungen und der Landnutzungsintensität (LUI) sowie deren Interaktionen auf die Anzahl der Arten (Poisson-Modell) und die kumulative Deckung der Moose (Binomialmodell) in den Jahren 2015 und 2016. Die vollständigen Modelle wurden vereinfacht, indem Terme entfernt wurden, die die Modelle unter Verwendung von Likelihood-Verhältnissen nicht signifikant verbesserten (entfernte Terme sind grau dargestellt). Die Schätzungen wurden für die reduzierten Modelle berechnet. Alle Modelle enthielten die Identität des jeweiligen Graslands, eingebettet in die Region, als Zufallsterm. R^2m wurde als marginaler Koeffizient (Anteil der Varianz, der allein durch feste Faktoren erklärt wird) und R^2c als bedingter Koeffizient (Anteil der Varianz, der sowohl durch feste Faktoren als auch durch Zufallsfaktoren erklärt wird) für alle gemischten Effektmodelle berechnet.

Number of species 2015	Estimate	Standard Error	*p*-value	R^2m	R^2c
Intercept	1.86	0.21		0.24	0.55
LUI	-0.48	0.10	<0.001 ***		
Disturbance	-0.56	0.07	<0.001 ***		
Seed addition			0.886		
Disturbance x Seed addition			0.904		
LUI x Seed addition			0.714		
Disturbance x LUI			0.706		
Disturbance x LUI x Seed addition			0.690		

Number of species 2016	Estimate	Standard Error	*p*-value	R^2m	R^2c
Intercept	2.10	0.24		0.21	0.64
LUI	-0.52	0.09	<0.001 ***		
Disturbance			0.794		
Seed addition			0.621		
Disturbance x Seed addition			0.933		
LUI x Seed addition			0.175		
Disturbance x LUI			0.946		
Disturbance x LUI x Seed addition			0.840		
Cover of species 2015	Estimate	Standard Error	*p*-value	R^2m	R^2c
Intercept	1.19	0.88		0.46	0.57
LUI	-2.07	0.65	<0.001 ***		
Disturbance	-2.28	0.60	<0.001 ***		
Seed addition			0.823		
Disturbance x Seed addition			0.939		
LUI x Seed addition			0.651		
Disturbance x LUI			0.780		
Disturbance x LUI x Seed addition			0.829		
Cover of species 2016	Estimate	Standard Error	*p*-value	R^2m	R^2c
Intercept	1.26	0.78		0.53	0.59
LUI	-1.76	0.46	<0.001 ***		
Disturbance	-3.28	0.77	<0.001 ***		
Seed addition			0.829		
Disturbance x Seed addition			0.913		
LUI x Seed addition			0.556		
Disturbance x LUI			0.701		
Disturbance x LUI x Seed addition			0.834		

Table 3. Results of the linear mixed effects model estimating the effect of disturbance on the Sørensen dissimilarity depending on year, seed addition, and land-use intensity (LUI). The model included region as a random term. R^2 was calculated as the marginal coefficient (proportion of variance explained by fixed factors alone) and R^2c as the conditional coefficient (proportion of variance explained by both, fixed and random factors) of determination.

Tabelle 3. Ergebnisse des linearen gemischten Effektmodells zur Schätzung des Einflusses von Störungen auf die Sørensen-Unähnlichkeit in Abhängigkeit von Jahr, Ansaat und Landnutzungsintensität (LUI). Das Modell enthielt die Region als Zufallsterm. R^2m wurde als marginaler Koeffizient (Anteil der Varianz, der allein durch feste Faktoren erklärt wird) und R^2c als bedingter Koeffizient (Anteil der Varianz, der sowohl durch feste Faktoren als auch durch Zufallsfaktoren erklärt wird) für alle gemischten Effektmodelle berechnet.

Disturbance effect on Sørensen dissimilarity	Estimate	Standard Error	*p*-value	R^2	R^2c
Intercept	0.491	0.049	<0.001 ***	0.17	0.18
Year	-0.205	0.028	<0.001 ***		
Seed addition plots	-0.018	0.028	0.518		
LUI	-0.052	0.020	0.010 *		

4. Discussion

Soil disturbance is a commonly used measure for the restoration of plant species richness in grasslands (Schnoor et al. 2015), and restoration success can be considerably improved when combined with seeding of targeted seed mixtures with plant species that are adapted to the local conditions (Bossuyt & Honnay 2008, Klaus et al. 2017, Freitag et al. 2021). However, soil disturbances can have unintended consequences, such as nutrient leaching (Klaus et al. 2018) and a reduction in the abundance of belowground organisms like soil nematodes and fungi (Resch et al. 2022). Such a detrimental effect of soil disturbance can also be expected for grassland bryophytes, which mainly colonize the ground of rather nutrient-poor grassland ecosystems. Here, we analysed the effects of grassland restoration using sward disturbance and/or seed addition on bryophyte communities in 72 grasslands managed at different intensities.

We found that both species richness and cover of grassland bryophytes strongly declined in the first year after sward disturbance. This is in line with Chytrý et al. (2001), who applied different disturbance types and even completely eliminated bryophytes and lichens with a rather drastic measure of sod cutting in heathlands of the Czech Republic. Similarly, Müller et al. (2014) found detrimental effects of experimental small-scale disturbances on bryophytes when creating more than 12% of bare ground in German agricultural grasslands.

In line with previous studies, we observed an overall decrease in bryophyte species richness and cover with increasing land-use intensity (Müller et al. 2012, Virtanen et al. 2017, Virtanen et al. 2025). In high land-use intensity grasslands, which are usually highly fertilized, only very few taxa such as *Brachythecium rutabulum* and *Eurhynchium* spp. can persist with low cover, as they are able to tolerate fertilization to a certain degree (Dirkse & Martakis 1992, Virtanen et al. 2000, Nebel & Philippi 2001). Furthermore, some short-lived species that are adapted to frequent disturbances by land-use interventions can occur in high land-use intensity sites. This well-known decline of species richness with increasing land-use intensity is explained by negative direct toxic fertilization effects (Carroll et al. 2000, Andersen et al. 2016, Lin et al. 2025), and indirect negative effects via increased vascular plant biomass and competition for light (Carroll et al. 2000, Bergamini & Pauli 2001, Virtanen et al. 2025). Consequently, we found stronger absolute losses in richness and cover in low land-use intensity sites compared to high land-use intensity sites, since land-use intensity generally strongly decreases richness and cover.

Concerning the short-term recovery of bryophyte communities, our results show that bryophyte richness was only temporarily affected and recovered already in the second year after disturbance, while bryophyte cover remained low. This contrasts with Chytrý et al. (2001), who used sod cutting as disturbance method, which can be considered much more drastic than harrowing. The authors reported a slower recovery of cryptogam species richness after sod cutting with long-term elimination of late-successional species. Interestingly, the recovery of bryophyte species richness was not affected by land-use intensity (non-significant disturbance x LUI interaction in 2016; Table 2), although one might assume that grasslands of high resident richness of bryophytes might have a lower relative recovery of bryophyte species richness (see Schäfer et al. 2019 for LUI effects on the recovery of vascular plant species richness). However, differing from the mentioned previous studies, in our case the topsoil was not completely removed and bryophytes likely recovered quickly from small bryophyte shoot fragments that remained on the ground, independent of land-use intensity. In addition, as the disturbed subplots were surrounded by undisturbed vegetation, it

might well be that species were able to colonize the disturbed areas from nearby source populations quicker than if such surrounding populations had been eradicated by larger scale disturbances.

Hydbom et al. (2012), who studied the effects of disturbances in degraded sandy grasslands of southern Sweden, even found increased bryophyte species richness four years after applying soil disturbances, mainly because of an increase of acrocarpous species associated with early succession stages and higher pH resulting from deep soil perturbation. Lin et al. (2025) found positive effects by small-scale disturbances on bryophyte richness in an experimental grassland site in Switzerland. A common explanation for the positive disturbance effect on bryophyte richness is that many bryophyte species, particularly small and short-lived ones that are weak competitors, but fast colonizers depend on patches of bare soil for colonization, which at the same time exhibit reduced competition by vascular plant species (Zechmeister & Moser 2001, Lin et al. 2025). However, while bryophyte species richness recovered quickly, we found that bryophyte cover remained reduced one year after disturbance. The full recovery of the bryophyte cover, which was mainly built up by pleurocarpous, late-successional species, probably takes more time. As vegetation cover was still not fully recovered in 2016, it might be that microclimatic changes partly hindered the colonization of some gaps because of physiological and ecological reasons: although bryophytes are poikilohydric and adapted to changing water conditions, alternating periods of desiccation and cessation of growth might have slowed down bryophyte establishment and growth in the agriculturally managed grasslands (Vanderpoorten et al. 2004), at least the late successional pleurocarpous mosses which are often adapted to more balanced moisture conditions. A removed bryophyte layer can further affect the composition of the vascular plant community (Janišová et al. 2025). As a consequence of such shifts in community composition and because ecosystem functions such as water and microclimate regulation as well as nutrient cycling can only be fully provided when bryophyte cover is well-developed (Turetsky 2003, Jaroszynska et al. 2023, Slate et al. 2024), it is likely that certain functions are limited until also bryophyte cover is fully restored.

Regarding our experimental plots, Klaus et al. (2017) and later also Freitag et al. (2021) showed that seeding in combination with sward disturbance increased vascular plant species richness. However, we found that seeding had no effect on the short-term recovery of bryophytes, which can be expected since only seeds of vascular plants were added. This contrasts with Lin et al. (2025) who found positive effects of increased vascular plant species richness from seeding on bryophyte species richness. The authors assumed that this positive effect might be on the one hand because communities with higher vascular plant richness create structurally more heterogeneous habitats providing different light niches with open and more shaded areas, as it is known from forest ecosystems (e.g. Helbach et al. 2022). On the other hand, diverse plant communities might improve the microclimate for bryophytes below the herbaceous layer that creates continuous but moderate shading also during dry seasons (Vanderpoorten, et al. 2004), which can cause lower temperatures and vapor pressure deficit at the soil surface and increase surface soil moisture (Cowles et al. 2016). However, as vegetation cover was fully recovered in 2016 (Schäfer et al. 2019) favourable conditions for bryophyte growth under increased vascular plant species richness should have been restored.

5. Conclusions

While bryophyte species richness recovered quickly from sward disturbance after one year, bryophyte cover did not. This indicates that grassland-restoration measures including disturbances and seed addition have no detrimental effects on bryophyte diversity. However, ecosystem functions provided by bryophytes might be limited until bryophyte cover is fully restored, which takes longer than the recovery of bryophyte diversity. This recovery of bryophyte cover, however, needs to be investigated in longer-term experiments including the measurement of functions supported by bryophytes.

Erweiterte deutsche Zusammenfassung

Einleitung – Halbnatürlichen Grasländer sind äußerst vielfältige Ökosysteme, die viele spezialisierte Arten beherbergen (Dengler et al. 2020, Biurrun et al. 2021) und wichtige Ökosystemfunktionen und -dienstleistungen erfüllen (Rounsevell et al. 2018). Sie sind auch räumlich relevant, da etwa 20 % der Paläarktis und etwa 15 % des gemäßigten Europas von Grasland bedeckt sind (Boch et al. 2020, Dengler et al. 2020). Moose sind oft ein wichtiger Bestandteil der Artenvielfalt in Grasländern (Biurrun et al. 2021). Darüber hinaus leisten Moose einen wichtigen Beitrag zu Ökosystemfunktionen, wie der Wasser- und Mikroklimaregulierung und dem Nährstoffkreislauf (Turetsky 2003, Jaroszynska et al. 2023, Slate et al. 2024).

In halbnatürlichen Grasländern gilt die Landnutzungsintensivierung als einer der Hauptfaktoren für die Degradierung von Lebensräumen, was zu einem Rückgang der biologischen Vielfalt führt (Rounsevell et al. 2018). Die Wiederherstellung der biologischen Vielfalt und der Ökosystemfunktionen in Grasländern nach Störungen, d. h. die Fähigkeit, zu früheren Zuständen zurückzukehren, ist aus wirtschaftlicher, aber auch aus naturschutzfachlicher Sicht von besonderer Bedeutung, da Ökosystemfunktionen die Bereitstellung von Ökosystemleistungen gewährleisten (Allan et al. 2015, Schäfer et al. 2019). Dementsprechend wird die Aussaat von Saatgutmischungen häufig zur Wiederherstellung von degradiertem Grasland eingesetzt, oft in Kombination mit Störungen der Grasnarbe, um den Erfolg der Etablierung zu erhöhen (Kiehl et al. 2010, Sommer et al. 2025). Während Grasnarbenstörungen zunächst drastische Auswirkungen auf Gefäßpflanzen haben, sind die Auswirkungen auf Moose weitgehend unklar. Auch ist unklar, ob die Zugabe von Saatgut die Erholung von Moosgemeinschaften und ihren Artenreichtum beeinflusst und welchen Einfluss dabei die Landnutzungsintensität in Interaktion mit Störungen spielt.

Das Ziel dieser Studie war es deshalb, die Auswirkungen von Störungen, einzeln und in Kombination mit der Zugabe von Saatgut, entlang eines Gradienten der Landnutzungsintensität auf die Artenvielfalt und Deckung von Moosen in landwirtschaftlichen Grasländern zu untersuchen.

Unsere Hauptfragen lauteten: (1) Wie werden die Artenvielfalt und die Deckung von Moosen durch Störungen der Grasnarbe und die Zugabe von Saatgut beeinflusst? (2) Erholen sich die Artenvielfalt und die Deckung von Moosen kurzfristig, d. h. innerhalb eines Jahres nach der Störung der Grasnarbe, und wird die Erholung durch die Zugabe von Saatgut beeinflusst? (3) Werden die Auswirkungen der Störung und die Erholung der Moosgemeinschaften durch die Landnutzungsintensität beeinflusst?

Untersuchungsgebiet – Die Studie wurde im Rahmen des Programms „Biodiversity Exploratories“ (www.biodiversity-exploratories.de; Fischer et al. 2010) in 72 landwirtschaftlichen Grasländern in drei Regionen Deutschlands durchgeführt: (i) Das UNESCO-Biosphärenreservat Schorfheide-Chorin im Nordosten Deutschlands. (ii) Der Nationalpark Hainich und seine Umgebung in Mitteldeutschland. (iii) Das UNESCO-Biosphärengebiet Schwäbische Alb in Südwestdeutschland. Die drei Untersuchungsgebiete unterscheiden sich hinsichtlich der Niederschlagmenge (abnehmend von SW nach NE), Jahresdurchschnittstemperatur (zunehmend von SW nach NE) und Höhe ü. NN (abnehmend von SW nach NE; Tab. 1). Dennoch weisen die Gebiete ähnliche Gradienten hinsichtlich der Landnutzungsintensität auf (Blüthgen et al. 2012).

Methode – Um die Auswirkungen von Störungen (Bodenbearbeitung mit einer Kreiselegge), einzeln und in Kombination mit Aussaat, entlang eines Gradienten der Landnutzungsintensität auf Moosgemeinschaften zu untersuchen, haben wir ein vollfaktorielles Experiment mit jeweils vier 7 m × 7 m großen Behandlungsteilflächen (Kontrolle, nur Aussaat, Aussaat und Störung, nur Störung) in 72 landwirtschaftlich genutzten Grasländern in Deutschland durchgeführt. In 2 m × 2 m großen Quadraten pro Behandlungsteilfläche haben wir alle Moose und ihre prozentuale Deckung über zwei Jahre hinweg erfasst (Abb. 1, 2). Die Landnutzungsintensität wurde durch die jährliche Befragung von Landwirten erhoben. Wir quantifizierten die Landnutzungsintensität für jedes Grasland nach Blüthgen et al. (2012) unter Verwendung eines integrierten Landnutzungsintensitätsmaßes, das die standardisierten Intensitäten der Düngung, die Häufigkeit der Mahd und die Weideintensität in den Jahren 2015 und 2016 quantifiziert. Die Berechnung der Landnutzungsintensität erfolgte unter Verwendung des in BExIS (http://doi.org/10.17616/R32P9Q) implementierten Berechnungstools (Ostrowski et al. 2020).

Wir verwendeten lineare gemischte Effektmodelle und verallgemeinerte lineare gemischte Effektmodelle (R-Paket lme4; Bates et al. 2015), um die Auswirkungen der Behandlungen und der Landnutzungsintensität auf den Artenreichtum und die Deckung der Moose in den Jahren 2015 und 2016 zu testen. Wir behandelten die Identität der 72 Graslandflächen, die in die drei Regionen eingebettet sind, als Zufallsfaktoren. Wir haben die einzelnen Behandlungen (Störung und Saatgutzugabe) und ihre Interaktionen (Störung × Aussaat) sowie die Landnutzungsintensität als feste Faktoren einbezogen.

Ergebnisse und Diskussion – Über einen Zeitraum von zwei Jahren und über alle 288 Teilflächen hinweg erfassten wir insgesamt 52 Moostaxa. Die Anzahl der Taxa pro Teilfläche reichte von 0 bis 15, mit einem Durchschnitt von 2,7 (± 2,3 SD) im Jahr 2015 und 4.0 (± 2,8 SD) im Jahr 2016. Die Artenvielfalt und Deckung der Moose war in Grasländern mit geringer Landnutzungsintensität höher als in solchen mit hoher Landnutzungsintensität (Abb. 3), was mit den Ergebnissen anderer Studien übereinstimmt (Müller et al. 2012, Virtanen et al. 2017, Virtanen et al. 2025). Darüber hinaus unterschied sich die Zusammensetzung der Moosgemeinschaften entlang des Landnutzungsintensitätsgradienten, wobei in Flächen mit hoher Landnutzungsintensität tendenziell mehr kurzlebige Arten (r-Strategen) vorkamen (Anhang E1). Der bekannte Rückgang der Artenvielfalt mit zunehmender Landnutzungsintensität lässt sich durch negative direkte toxische Düngungseffekte (Carroll et al. 2000, Andersen et al. 2016, Lin et al. 2025) und indirekten negativen Auswirkungen durch erhöhte Biomasse von Gefäßpflanzen und Konkurrenz um Licht erklären (Carroll et al. 2000, Bergamini & Pauli 2001, Virtanen et al. 2025).

Störungen führten zu einer starken Abnahme der Artenvielfalt und der Deckung der Moose (Abb. 3a, Tab. 2), sowie zu einer hohen Sørensen-Unähnlichkeit zwischen gestörten und ungestörten Teilflächen (Abb. 4, Tab. 3). Chytrý et al. (2001), eliminierten Moose sogar vollständig durch eine ziemlich drastische Maßnahme, nämlich das Abtragen von Grasnarben in Heidegebieten der Tschechischen Republik. In ähnlicher Weise stellten Müller et al. (2014) in deutschen Grasländern negative Effekte experimenteller kleinräumiger Störungen auf Moose fest, wenn mehr als 12 % des Bodens freigelegt wurden. Während in unserer Studie die Artenvielfalt und die Deckung der Moose mit zunehmender Landnutzungsintensität stark abnahmen (Tab. 2), war der Rückgang der Artenvielfalt aufgrund von Störungen am stärksten bei geringer Landnutzungsintensität, wo die Artenvielfalt der Moose im Allgemeinen höher war.

Im zweiten Jahr des Experiments fanden wir zwischen gestörten und ungestörten Teilflächen keine Unterschiede mehr in der Moosartenvielfalt (Abb. 3c, Tab. 2). Auch die Artenzusammensetzung zwischen gestörten und ungestörten Teilflächen wurde ähnlicher (Abb. 4, Tab. 3), was auf eine Erholung der Gemeinschaften hindeutet. Interessanterweise hatten die Landnutzungsintensität und die Aussaat keinen signifikanten Einfluss auf die Erholung der Artenvielfalt und Deckung der Moose (Tab. 2). Die schnelle Erholung der Moosartenvielfalt steht im Gegensatz zu Chytrý et al. (2001), die wesentlich drastischere Störungsmethoden als wir anwendeten. Die Autoren berichteten von einer langsameren Erholung der Moosartenvielfalt mit einer langfristigen Eliminierung von Arten der späten Sukzessionsphase. In unserem Fall wurde aber der Oberboden nicht vollständig entfernt, und die Moose erholten sich wahrscheinlich unabhängig von der Landnutzungsintensität schnell aus kleinen Sprossfragmenten, die auf dem Boden zurückblieben. Da die gestörten Teilflächen zudem von ungestörter Vegetation umgeben waren, ist es gut möglich, dass Arten die gestörten Flächen schneller aus nahegelegenen

Ausgangspopulationen besiedeln konnten, als wenn diese umgebenden Populationen durch großflächigere Störungen eliminiert worden wären. In unserer Studie erholte sich die Moosdeckung jedoch noch nicht nach einem Jahr (Abb. 3d, Tab. 2). Die vollständige Wiederherstellung der Moosdeckung, die hauptsächlich aus pleurokarpen Arten der späten Sukzessionsphase bestand, dauert wahrscheinlich länger. Da sich die Vegetationsdecke 2016 noch nicht vollständig erholt hatte, könnte es sein, dass mikroklimatische Veränderungen die Besiedlung einiger Lücken aus physiologischen und ökologischen Gründen teilweise behindert haben: Obwohl Moose poikilohydrisch sind und sich an wechselnde Wasserbedingungen anpassen können, könnten abwechselnde Perioden der Austrocknung und des Wachstumsstillstands die Etablierung und das Wachstum von Moosen in landwirtschaftlich genutzten Grasländern verlangsamt haben (Vanderpoorten et al. 2004), zumindest bei den pleurokarpen Arten der späten Sukzessionsphase, die oft an ausgeglichenere Feuchtigkeitsbedingungen angepasst sind.

Schlussfolgerung – Die schnelle Erholung der Artenvielfalt der Moose deutet darauf hin, dass Maßnahmen zur Wiederherstellung von Grasland, einschließlich Störungen und Saatgutzugabe, offenbar keine nachteiligen Auswirkungen auf die Moosartenvielfalt haben. Die von Moosen bereitgestellten Ökosystemfunktionen könnten jedoch begrenzt sein, bis die Moosdeckung vollständig wiederhergestellt ist. Die Erholung der Moosdeckung muss in längerfristigen Experimenten weiter untersucht werden, einschließlich der Messung der von Moosen unterstützten Ökosystemfunktionen.

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Author contributions

NH, DP, TK and VHK conceived and designed the seed addition and disturbance experiment. SB developed the initial concept of this study involving bryophytes. DP and VHK coordinated the disturbance experiment and the seed addition in the field. SB carried out the bryophyte surveys. NP analyzed the data. SB, NP and VHK wrote the first draft of the paper. All authors contributed to the final manuscript.

Data availability statement

The dataset is publicly available via the Biodiversity Exploratories Information System (https://doi.org/10.71615/bexis.32174-5; Boch 2025).

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. NMDS of the recorded bryophyte species colored by life history strategy.

Anhang E1. NMDS der erfassten Moosarten, farblich nach Lebensstrategien dargestellt.

Supplement E2. NMDS of the bryophyte communities along the land-use intensity gradient.

Anhang E2. NMDS der Moosgemeinschaften entlang des Landnutzungsintensitätsgradienten.

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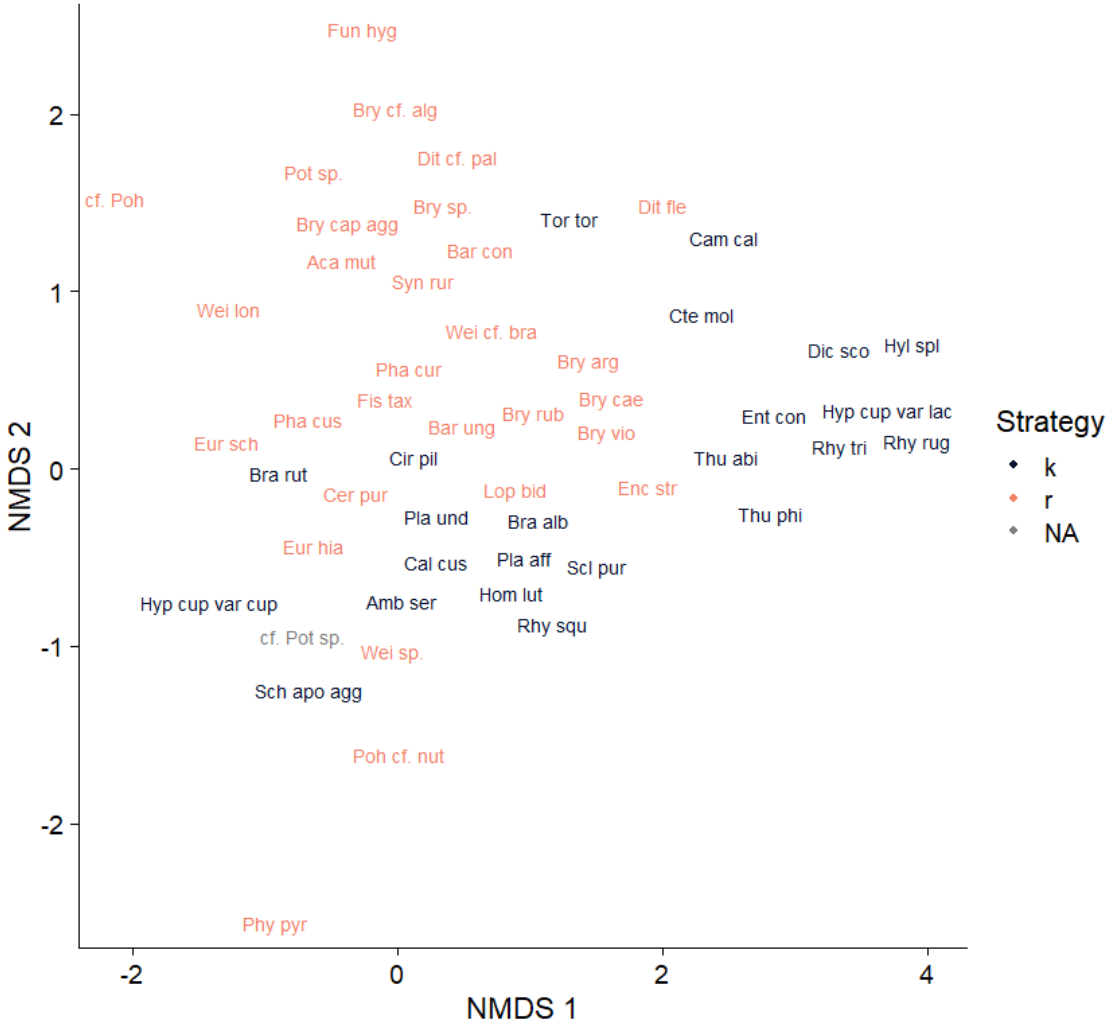
Supplement E1. NMDS (Oksanen et al. 2025) of the recorded bryophyte species (abbreviated names) colored by life history strategy (k and r strategy according to Van Zuijlen et al. 2023). The position of the species represents their average in the multidimensional space. The x-axis basically shows a decreasing land-use intensity.

Anhang E1. NMDS (Oksanen et al. 2025) der erfassten Moosarten (abgekürzte Namen), farblich nach Lebensstrategien (k- und r-Strategie gemäß Van Zuijlen et al. 2023) dargestellt. Die Position der Arten entspricht ihrem Durchschnittswert im mehrdimensionalen Raum. Die x-Achse zeigt im Wesentlichen eine abnehmende Landnutzungsintensität.



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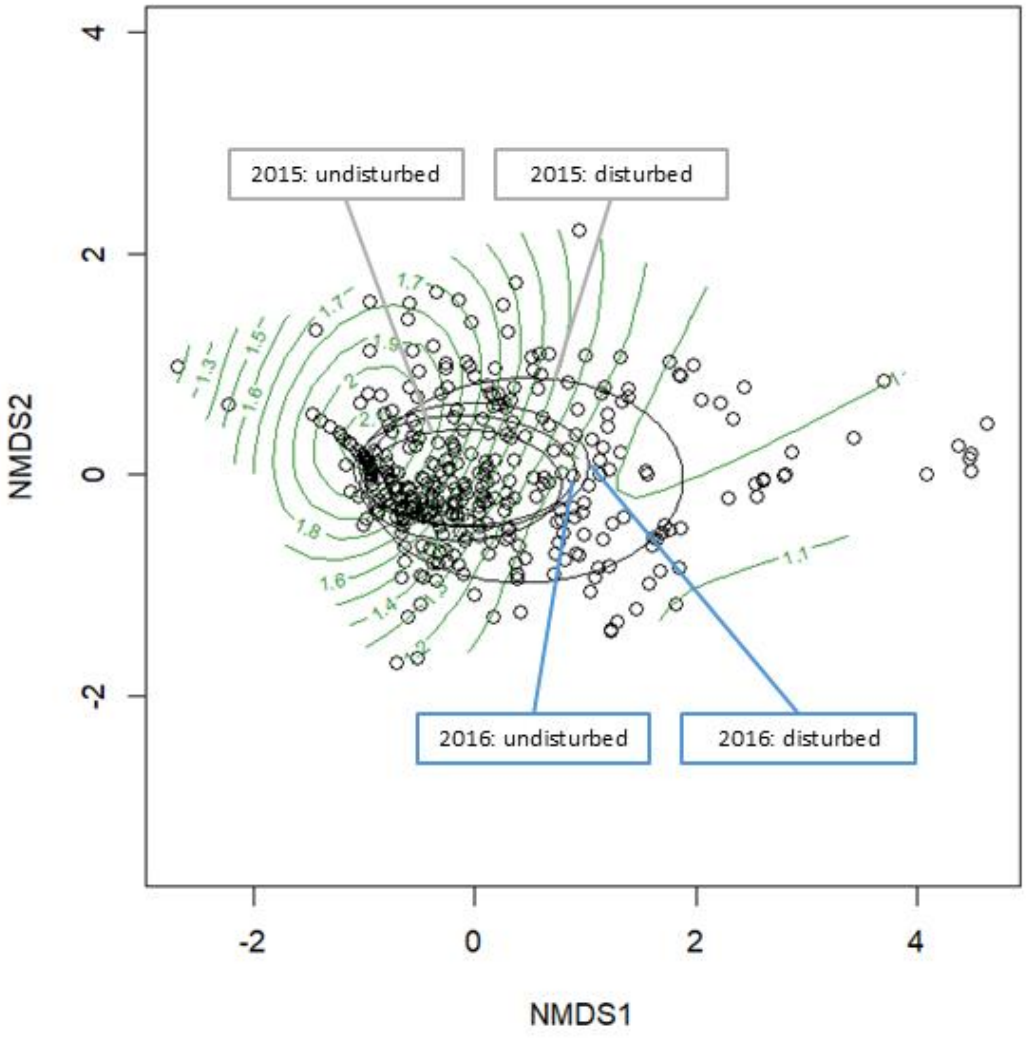
Supplement E2. NMDS (Oksanen et al. 2025) of the bryophyte communities (circles) along the land-use intensity gradient (green lines). In addition, ellipses indicate differences of disturbed and undisturbed communities, showing large differences between undisturbed and disturbed communities in 2015. In 2016 the differences largely disappeared, indicating a recovery of communities towards the initial bryophyte species composition.

Anhang E2. NMDS (Oksanen et al. 2025) der Moosgemeinschaften (Kreise) entlang des Landnutzungsintensitätsgradienten (grüne Linien). Darüber hinaus zeigen Ellipsen Unterschiede zwischen gestörten und ungestörten Gemeinschaften an, wobei 2015 große Unterschiede zwischen ungestörten und gestörten Gemeinschaften zu verzeichnen waren. Im Jahr 2016 verschwanden diese Unterschiede weitgehend, was auf eine Erholung der Gemeinschaften hin zur ursprünglichen Moosartenzusammensetzung hindeutet.



Supplement literature

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