Journal of Applied Ecology

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Journal:	*Journal of Applied Ecology*
Manuscript ID	Draft
Manuscript Type:	Research Article
Date Submitted by the Author:	n/a

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Key-words:	dispersal limitation, fertilization, functional traits, land-use intensity, productivity, seed addition, seedling establishment, trait-environment interactions

Restoration of permanent grasslands by seeding: assessing the limiting factors along land-use gradients

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ABSTRACT

1. Land-use intensification caused dramatic declines in grassland biodiversity in the past decades, which in Europe could not yet be halted by agri-environmental schemes. Restoration of plant species richness in permanent grasslands is a major topic in nature conservation. As species richness is often limited by seed availability, the introduction of locally absent species is crucial. Seeding diverse mixtures is a commonly used approach to overcome seed limitation, but restoration outcomes are highly variable. It remains hardly understood how land-use intensity constrains restoration and how plant traits could be considered in this respect to increase restoration success.
2. We established a full-factorial experiment with diverse seeding and topsoil disturbance in 73 permanent grasslands along a land-use intensity and productivity gradient and compared the restoration success over five years. We related the number of established species after five years to land-use intensity and productivity and tested whether specific plant functional traits promoted the establishment of sown plant species in interaction with productivity.
3. Both seeding and disturbance had positive effects on plant diversity, with the strongest positive effect in the combined treatment. We found no direct effects of land-use intensity. However, fertilization indirectly limited establishment of sown species in the combined treatment through a negative effect of productivity on the number of established species.
4. Plant traits affected sown species' establishment especially in the seeding and disturbance treatment, but these effects varied with productivity. Low trait values for height, seed mass and specific leaf area increased the establishment success in low-productive grasslands, whereas species with higher seed mass and higher specific leaf area established better at high productivity.
5. *Synthesis and applications.* Given the availability of appropriate, e.g. locally adapted, seed material, our results showed that the increase in plant species richness can be considerable and quick when prior sward disturbance is applied prior seeding. Productivity is a suitable

indicator for the restoration outcome and can be used to compile site-specific seed mixtures, yet large shares of variation in restoration success remain unknown. Restoration via seeding should focus on low-productive grasslands, where low-competitive sowing species match the resident vegetation.

INTRODUCTION

Land-use intensification has dramatically impacted both biodiversity and ecosystem service provision of permanent grasslands (IPBES, 2019; Newbold et al., 2016). Europe, for example, faced alarming declines in grasslands area and deteriorations in conservation status, which could not yet be halted by agri-environmental schemes (Janssen et al., 2016). Especially intensive fertilization and frequent mowing lead to severe declines in plant species richness (Gross, Bloor, Louault, Maire, & Soussana, 2009; Socher et al., 2012) such that even common plant species decrease in abundance at alarming rates (Jansen, Bonn, Bowler, Bruelheide, & Eichenberg, 2019). Grasslands therefore are a major target of restoration (IPBES, 2018; Pywell et al., 2002). Yet, prediction of restoration success is often inaccurate because outcomes can vary greatly among restoration efforts, driven by variation in the constraining factors such as restoration actions or site conditions (Brudvig et al., 2017).

The restoration of local plant species richness in grasslands may be strongly limited by the availability of seeds (Clark, Poulsen, Levey, & Osenberg, 2007; Myers & Harms, 2009) because most grassland species are short-distance seed dispersers (Coulson, Bullock, Stevenson, & Pywell, 2001; Sperry et al., 2019) and do not form persistent soil seed banks (Kiss, Deák, Török, Tóthmérész, & Valkó, 2018; Klaus, Hoever et al., 2018). Therefore, a mandatory step to restore plant species richness is to actively introduce locally absent species, for example by seeding diverse seed mixtures (Carter & Blair, 2012). Compared to elaborate techniques to restore a specific taxonomic composition, such as fresh hay transfer (Kiehl, Kirmer, Donath, Rasran, & Hölzel, 2010), sowing commercially available seeds of species of regional provenance is relatively easy and could be implemented in agricultural routines at larger scales to increase the taxonomic and functional diversity. Grassland restoration by sowing has been successfully applied on ex-arable land (Carter & Blair, 2012; Pywell et al., 2002; Wagner et al., 2020) and in low- and high-productive grasslands (Foster & Tilman, 2003; Pywell et al., 2007; Zobel, Otsus, Liira, Moora, & Möls, 2000). Yet, most studies include only few sites, which makes it difficult to assess the significance of constraining factors in restoration beyond a mere comparison among sites.

In the early germination and seedling stages of a plant, safe microsites such as gaps within the established vegetation are also crucial for successful recruitment (Münzbergová & Herben, 2005). Technically, topsoil disturbance can be used to create gaps in the established sward, which enables seed-soil contact and amplifies the germination of sown seeds through increased light availability at the soil surface (Bischoff, Hoboy, Winter, & Warthemann, 2018; Myers & Harms, 2009). However, despite its practical relevance it largely remains unclear to what degree plant species richness can be restored and how land-use intensity in regularly used permanent grasslands affects the restoration success. To ensure efficient biodiversity restoration, we still need to learn about the constraints in the long-term success of plant establishment across a wide range of local factors, such as productivity and land use that are typical for permanent grasslands.

Practitioners are aware that the establishment success of reintroduced plant species is highly species-specific (e.g. Engst, Baasch, & Bruelheide, 2017), but the reasons are often unknown. Plant functional traits are increasingly considered to select suitable species for restoration (Laughlin, 2014; Zirbel, Bassett, Grman, & Brudvig, 2017), and a trait-based selection of candidate species might increase the rates of successful establishment. Traits such as canopy height, specific leaf area and seed mass reflect trade-offs in plant strategies linked to competition and reproduction (Westoby, 1998). Pywell et al. (2003) for example have shown that competitive species have an advantage to establish in productive grasslands, but restoration success is likely dependent on the match between the environment and suitable plant functional traits (Balazs et al., 2020). Accounting for traits and trait-interactions with productivity and land-use intensity in permanent grasslands could result in concrete recommendations to select species that match local site conditions and hence increase restoration success.

We aimed to assess the long-term restoration success using a species-rich and regionally adapted seed mixture along gradients of land-use intensity and productivity, with or without prior topsoil disturbance. We established a full-factorial experiment in 73 grasslands ranging from low-productive sheep pastures to high-productive, agriculturally improved grasslands. Short-term results from this experiment showed that intensively used, species-poor grasslands increased strongly in species richness when a combination of seeding and disturbance was applied, while seeding alone had no effect on plant diversity (Klaus et al., 2017). Here, we assess how land use, productivity and specific plant functional traits relate to the long-term establishment of the introduced species. Specifically, we ask

- How effective is restoration by seeding, disturbance or their combination in enhancing plant species richness in the long run?
- To which degree do high levels of land-use intensity and productivity constrain the establishment of sown species in permanent grasslands?
- Which traits favour the establishment in permanent grasslands across the gradient of land-use intensity and productivity?

METHODS

Study design

We analysed five years of data of a seeding and disturbance experiment in 73 grasslands in the framework of the Biodiversity Exploratories, a large-scale and long-term research platform (M. Fischer et al., 2010). We installed the experiment in three German regions that span gradients in soil characteristics, elevation and climate and are representative of large parts of Central Europe. The regions comprise i) the calcareous mid-mountain range Biosphere Reserve Schwäbische Alb (48.4°N, 9.4°E), ii) the calcareous low-mountain range National Park Hainich-Dün and surroundings (51.1°N, 10.4°E) and iii) the postglacial landscape of Biosphere Reserve Schorfheide-Chorin (53.0°N, 14.0°E). While in the Schwäbische Alb and Hainich-Dün grasslands are restricted to mineral soils, some grasslands in Schorfheide-Chorin are situated on drained fen soils (M. Fischer et al., 2010). Within each region, we selected 23-25 permanent grasslands along gradients of land-use intensity and plant diversity, spanning from sheep pastures with up to 80 plant species per 16 m² to frequently mown improved grasslands with as few as ten plant species per 16 m². To quantify land-use intensity, farmers were interviewed each year about the amount of fertilizer used (kg N*ha^{-1}), the mowing frequency per year and the grazing intensity (livestock unit*grazing days*ha^{-1}) (Vogt et al., 2019). Here, we used averages of fertilization, mowing and grazing intensities from 2014 to 2018.

We established a 2*2 factorial experiment with seeding and soil disturbance treatments in 73 grasslands. The experimental plots were 7 m*7 m in size and were arranged in a row or a quadrat with 2 m distance between plots. In October 2014, we applied the disturbance treatment by mechanical perturbation of the sward and the topsoil down to 10 cm with a rotary harrow or a rotary cultivator. The topsoil disturbance created a high proportion of bare ground (ca. 50% in the following spring, Schäfer et al., 2019) and was relatively harsh compared to common agricultural re-seeding practices. We did not remove root and shoot fragments of the disturbed sward, so plants could possibly regrow. See Klaus et al. (2017) for further details on the design.

We used high-diversity and regionally adapted seed mixtures (Bucharova et al., 2017). The mixtures consisted of common and less-common species, which were selected from the grassland species pools for each region separately (M. Fischer et al., 2010). The mixtures included grasses, legumes and forbs and the amount of sown seeds per species depended inversely on the seed weight of the respective species. Two thirds of the mixture were sown in November 2014 and one third was sown in March 2015. In total, we sowed 5.37 g m^{-2} and 66 species in Schwäbische Alb, 4.11 g m^{-2} and 52 species in Hainich-Dün and 3.47 g m^{-2} and 47 species in Schorfheide-Chorin (no legumes were available in this region).

We surveyed vegetation and aboveground productivity from 2015 to 2019 annually in May before the first mowing or grazing management. Within the four experimental plots of the 73 grasslands, we recorded all vascular plant species on 2 m*2 m and estimated percentage cover. In 2018, we could not access three grasslands due to early land use. In total, this sums up to 1448 observations. As a proxy for productivity under untreated conditions, we annually clipped all living plant biomass of one square meter (four 0.25m^2 quadrats) on the control plots. We dried the biomass for 48 h at 80 °C and weighed it to the nearest gram.

Analysis

Seeding and disturbance effects on plant diversity

To analyse how seeding and disturbance affected plant diversity over time, we modelled species richness and Shannon diversity (Spellerberg & Fedor, 2003) as a function of the three-way interaction of seeding, disturbance and sampling year. Species richness was modelled as Poisson distributed with log-link while Shannon diversity was modelled as Gaussian. Sampling year was treated as categorical, because effects over time were non-linear. We included varying intercepts for grassland site to account for the experimental design and varying intercepts for year within region (five years times three regions), because weather conditions and survey teams varied between years and regions. The multi-level regression model was estimated in a hierarchical Bayesian framework using the Stan probabilistic language (Stan Development Team, 2020) accessed via the package *brms* v2.12 (Bürkner, 2017) in R v3.6.3 (R Core Team, 2018). For this and all following models, we specified weakly informative normal priors with zero mean for fixed parameters and default vague priors for the intercepts (see Appendix). We run this and the following models with six parallel chains and 25,000 iterations (12,500 discarded as burn-in) and ensured convergence with R-hat values being <1.01 for all parameters. Model fit was assessed with posterior-predictive checks of residuals using the *bayesplot* package (Gabry & Mahr, 2019; Gabry, Simpson, Vehtari, Betancourt, & Gelman, 2019). We calculated a Bayesian R^2 accounting for varying intercepts (Gelman, Goodrich, Gabry, & Vehtari, 2019) and extracted the 90% credible interval for the posterior samples, which do not overlap zero when 95% of the posterior is either above or below zero.

Direct and indirect effects of land use on enrichment effect

To test how land-use intensity and site conditions moderate seeding effects on species richness (difference between seeding treatments and control, i.e. Δrichness) in the first year and in the fifth year, we fitted two separate multivariate models for seeding only and the seeding and disturbance treatments. Multivariate models sample the parameters jointly for the sub-models and thus allow modelling non-independent response variables measured on the same experimental unit. In both models, we modelled Δrichness of year one and year five as the absolute difference in species richness of the respective treatment to the control. We expected direct effects of grazing intensity, mowing frequency, productivity and region on Δrichness as well as an autoregressive effect of Δrichness of year one on year five (see also Fig. 3). Because fertilization intensity (log-transformed Nitrogen per hectare) was closely correlated to mowing frequency ($\rho=0.66$, Vogt et al., 2019), we included only an indirect effect of fertilization on Δrichness via productivity. We modelled productivity with Gamma distribution and log-link and assumed Gaussian errors for Δrichness in year one and year five. The repeated biomass measurements were simultaneously modelled as arising from a normal distribution with a mean equal to the 'true' latent productivity of each grassland and measurement error σ. The arithmetic means and standard deviations of harvested biomass were used as informative priors for the means of latent productivity, i.e. the priors varied between grasslands. We chose a weakly informative prior for the measurement error σ (see Appendix). The multivariate models were estimated using *rstan* v2.19.3 (Stan Development Team, 2020).

Plant functional traits effects on establishment

To explore how plant functional traits affect the establishment of sown plant species five years after seeding along land-use gradients, we modelled establishment of the sown plant species with logistic regression. We assumed sown plant species to have successfully established in the seeding treatments subplots when they were present in year five. Because we have no information which plant individuals grew on the subplots prior the experiment, we omitted presence or absence observations of sown species in grasslands when they were present on either the control or disturbance only subplots in any year. We kept 2767 observations, because sown species were present in the respective grassland in 36% of the cases in the Schwäbische Alb region, 35% in the Hainich-Dün and 21% in the Schorfheide region (see Appendix). This procedure is conservative especially for common species but reduces the number of false positive observations where a sown species was already present. From the LEDA

Traitbase (Kleyer et al., 2008) we extracted specific leaf area (relative growth rate), canopy height (competitive ability of the adult plant) and seed mass (energy for seedling recruitment).

We modelled binary establishment with logit link function as a function of specific leaf area, height, seed mass, productivity (the latter three log-transformed) and interactions of the traits with productivity because we assumed trait-environment-interactions. We included varying intercepts for species' identity and grassland site due to the multi-level structure and scaled all predictors to unit standard deviation. Productivity was again modelled as latent as in the multivariate models (see Appendix).

RESULTS

Seeding and disturbance had positive effects on plant diversity over the five years of this study, with the strongest positive effect in the combined treatment (Fig. 1a). Average plant species richness was 24.7 species per 4 m^2 on the control plot in the 73 grasslands. The effect of the seeding only treatment constantly increased from Δrichness near zero in the first year to 3.5 more species per 4 m^2 compared to the control (plus 15%) in the fifth year, but in combination with disturbance Δrichness was much higher (plus 9.3 species and 38% in the fifth year). The interactive effect of seeding and disturbance was however strongest in the second year and slightly decreased thereafter (Fig. 1a, see Table S1 for details). The abundance-weighted Shannon diversity showed very similar patterns, but the weak effect of seeding only on Δrichness suggests that the sown species still have little cover (Fig. 1b).

We found no direct effects of land-use measures on Δrichness, but fertilization indirectly limited establishment of sown species in the combined treatment through a negative effect of productivity on Δrichness (Fig. 2 b, Fig. 3 b). Δrichness in the first year did not depend on land use or productivity, which is underlined by low R^2 for both treatments (Fig. 2 a, b; Table 1). However, the negative effect of productivity on Δrichness in the fifth year suggests that productivity limits the long-term establishment of the sown species. Effects in the seeding only treatment were weaker (Table 1), which had a generally low Δrichness. Both productivity and Δrichness differed between regions (Table 1). In the fifth year, the least productive region (Hainich) had the highest increases in species richness in both seeding treatments, while the most productive region (Schorfheide) showed the smallest Δrichness (Table 1, Fig. 3 b).

Plant functional traits significantly influenced sown species' establishment, but effects of traits on establishment changed with productivity. Productivity, specific leaf area and their interaction were consistent predictors of establishment (Fig. 4, see Table S2 for details). Productivity decreased establishment drastically that the probability of successful establishment in year five was almost zero in productive grasslands (Fig. 5). Trait-productivity interactions indicate that species with high specific leaf area established better at high productivity, but species with low specific leaf area established better in low-productive grasslands in both seeding treatments (Fig. 5 a, b). For the seeding and disturbance treatment, small species with a low seed mass and low specific leaf area had on average a higher establishment success (Fig. 4). Low trait values for height, seed mass and specific leaf area increased the establishment success in low-productive grasslands, but species with higher seed mass and higher specific leaf area still established better at high productivity (Fig. 5 b).

In general, uncertainty in parameters was higher and average establishment success lower on the seeding only treatment (Fig. 4, Table S2). The marginal Bayes R^2 accounting for traits and productivity only, was considerably lower than the conditional R^2 for both seeding treatments (Table S2; seeding only: median R^2_{marg}=0.17, R^2_{cond}=0.46; seeding and disturbance: median R^2_{marg}=0.22, R^2_{cond}=0.41), which implies that grassland site and species identity accounted for a considerable share of variance that could not be explained by plant functional traits.

DISCUSSION

The ongoing biodiversity crisis is an urgent appeal to restore plant species richness in grasslands wherever possible. Our results highlight the high restoration potential of diverse seed mixtures for many permanent grasslands, especially when combined with soil disturbance. The boosting effect of disturbance on the establishment of sown species concurs with previous research (Bischoff et al., 2018;

Myers & Harms, 2009), but seeding only could also be considered if short-term success is not needed. We show that restoration success is especially high at low productivity levels (aboveground biomass below ca. 250 g m^{-2}) and that plant functional traits can help to select species for successful restoration along the productivity gradient.

The combination of seeding and disturbance was found to be the most effective method to increase plant diversity in most grasslands. This finding confirms previous studies stating that grassland plant species richness is largely limited by the availability of seeds due to dispersal limitation and the lack of a persistent soil seed bank of most grassland species (Clark et al., 2007; Klaus, Hoever et al., 2018; Myers & Harms, 2009). In line with early results from this experiment (Klaus et al., 2017), the combined treatment remained most effective throughout the course of the experiment. However, after 5 years plant species richness increased in the seeding only treatment as well. Concurrently, Harvolk-Schöning, Michalska-Hejduk, Harnisch, Otte, and Donath (2020), who used fresh hay to introduce species into established, species-poor grasslands, found no differences in restoration success between previously rotovated topsoil plots and plots that were only mown prior to hay transfer after 14 years. This suggests that the long-term establishment of transferred seeds does not necessarily depend on soil disturbance. The decreasing differences in species richness between both seeding treatments suggests that the creation of microsites is important for seeds to germinate and establish quickly, but for the long-term restoration success soil disturbance might not be necessary. Because soil disturbance prior to seeding means additional costs and labour, seeding only could be considered under low productive conditions or when the budget is small and quick restoration success is not necessary. Seeding only would also avoid negative environmental impacts of severe soil disturbance such as CO_2 emissions to the atmosphere and nitrate losses to the groundwater as a consequence of the decomposing vegetation sward (Klaus, Kleinebecker et al., 2018; Merbold et al., 2014).

Disturbance freed the seedlings from competition by plants already established in the sward irrespective of productivity, but not all species that germinated established in the longer term. Especially the intensively used, productive grasslands, which benefitted most at first (Klaus et al., 2017), lost previously germinated species. Between the first and the fifth year of the experiment, the relationship between productivity and the number of established species turned from neutral to negative, especially in the combined treatment where the initial species gain was highest. Similarly, other studies found smaller seeding successes in productive grasslands (Dickson & Foster, 2008; Foster, 2001). The increasing impact of productivity over time on establishment in our study clearly suggests that plant species enrichment by seeding is only an ephemeral success in productive grasslands and highlights that establishment limits species richness stronger than the availability of seeds (Clark et al., 2007). Concurrently, the number of newly established species correlated positively with the resident species richness (see Appendix). Similar to the drivers of the current diversity of the grasslands under study (Socher et al., 2012), land use had no direct effects on the long-term establishment, but fertilization limits establishment via productivity. This means that both species richness and the potential to introduce new species decrease with land-use intensity via its effect of fertilization on productivity. Here, productivity is mainly a result of soil fertility, which has been hypothesized to be among the most important constraints in the restoration of species-rich grasslands (Dickson & Foster, 2008; Walker et al., 2004). However, we are not able to identify a distinct threshold of productivity at which restoration would be successful or limited. Our results suggest that the establishment success is generally low at productivity levels above 250 g m^{-2} aboveground biomass in May, but the individual establishment success probably still depends on local site characteristics. We conclude that, to effectively restore productive species-poor grasslands, productivity must be reduced. The main focus for restoration in productive grasslands therefore must be to stop fertilization and reduce the soil nutrient loads, before fine-tuning the grazing and mowing management.

Plant functional traits clearly affected establishment. Sown species with a low specific leaf area consistently established better in low-productive grasslands. However, the patterns we observed at the seeding only treatment were less clear, probably due to the generally lower establishment rates and subsequently greater uncertainty in the relationships between traits and establishment. When seeding was combined with disturbance, we also found that less competitive species with low canopy height and low seed mass (such as *Dianthus carthusianorum* or *Sanguisorba minor*) established better. *Silene vulgaris*, *Primula veris* and *Briza media* established in even more than 25% of all grassland sites, which is a considerable rate for the rather small survey plot-size of 4 m² given the sward and sowing heterogeneity. These main effects could be driven by the fact that most species established in low-productive grasslands, where the plant community is already characterized by conservative slow-growing species (Allan et al., 2015).

The relevance of specific functional traits for establishment considerably interacted with productivity. On the combined treatment, competitive seedlings with high seed mass and fast-growing species with high specific leaf area established better in productive sites, while less competitive species established better at low productivity. Our results confirm previous research, where competitive species with large seeds showed higher recruitment rates (Clark et al., 2007) and established better in urban grassland restoration (L. K. Fischer, Lippe, & Kowarik, 2013) due to more energy stored in the seed. Species with high specific leaf area reflect a fast resource-acquisition strategy and thus increase the chance of sown species to survive in dense vegetation swards in the long-term (Engst et al., 2017). Contrastingly, species with low specific leaf area had an advantage in less managed urban grasslands (L. K. Fischer et al., 2013). Variation in establishment success along environmental gradients and trait-environment interactions in restoration are rarely studied. Our results suggest that species with low specific leaf area and low seed mass have an advantage in low-productive grasslands, where competitive plants lose their advantage, similar to research from North-American dry grasslands where species with low specific leaf area established better under high light conditions (Zirbel & Brudvig, 2020). Taken together, sown species are filtered by productivity in permanent grasslands and most likely reflect the traits of the resident plant community (Breitschwerdt, Jandt, & Bruelheide, 2015) by fast-growing tall species in high-productive, and slow-growing species in low-productive grasslands. We therefore second the call by Balazs et al. (2020) to compile site-specific seed mixtures to match the traits of resident vegetation and hence improve restoration success.

RECOMMENDATIONS FOR RESTORATION

Seeding diverse seed mixtures is an effective method to enhance plant diversity in permanent grasslands and can be as effective as fresh hay transfer (Wagner et al., 2020). We showed that the increase in species richness is considerable and quick when prior sward disturbance is applied. But in some settings without the need for immediate results, the cheaper and less destructive option of seeding only could be considered. Seeding and topsoil disturbance is easy to implement in agricultural routines given the availability of appropriate, e.g. locally adapted, seed material (Ladouceur et al., 2018). Because grassland productivity shapes plant community composition and determines the resident species richness (Socher et al., 2012) as well as establishment success, productivity is a suitable indicator whether restoration is reasonable and which species should be sown.

ACKNOWLEDGEMENTS

We thank Judith Hinderling, Torsten Meene, Svenja Kunze and many students for help during fieldwork. We also thank the managers of the three Exploratories, Kirsten Reichel-Jung, Iris Steitz, Sandra Weithmann, Florian Straub, Katrin Lorenzen, Juliane Vogt, Martin Gorke and Miriam Teuscher for their work in realizing this experiment and maintaining the plot and project infrastructure, Christiane Fischer and Jule Mangels for giving support through the central office, Michael Owonibi and Andreas Ostrowski for managing the central data base, and Eduard Linsenmair, Dominik Hessenmöller, Jens Nieschulze, Francois Buscot, Ernst-Detlef Schulze, Wolfgang W. Weisser, and the late Elisabeth Kalko for their role in setting up the Biodiversity Exploratories project. The work has been funded by the German Research Foundation (DFG) Priority Program 1374 'Infrastructure-Biodiversity-Exploratories' (FI 1246/15-2; HA 4597/6-3; HO 3830/2-4; KL 2265/4-4, PR 728/2-3). Field work permits were issued by the responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg (according to § 72 BbgNatSchG).

AUTHORS' CONTRIBUTIONS

D.P., U.H., N.H., V.K., T.K. and M.F. conceived the ideas and designed the experiment, V.K., D.S., R.B. and M.F. collected the data, M.F. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

All data and code used for this study will be archived within the BExIS database of the Biodiversity Exploratories project (https://bexis.uni-jena.de/PublicData).

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FIGURES AND TABLES

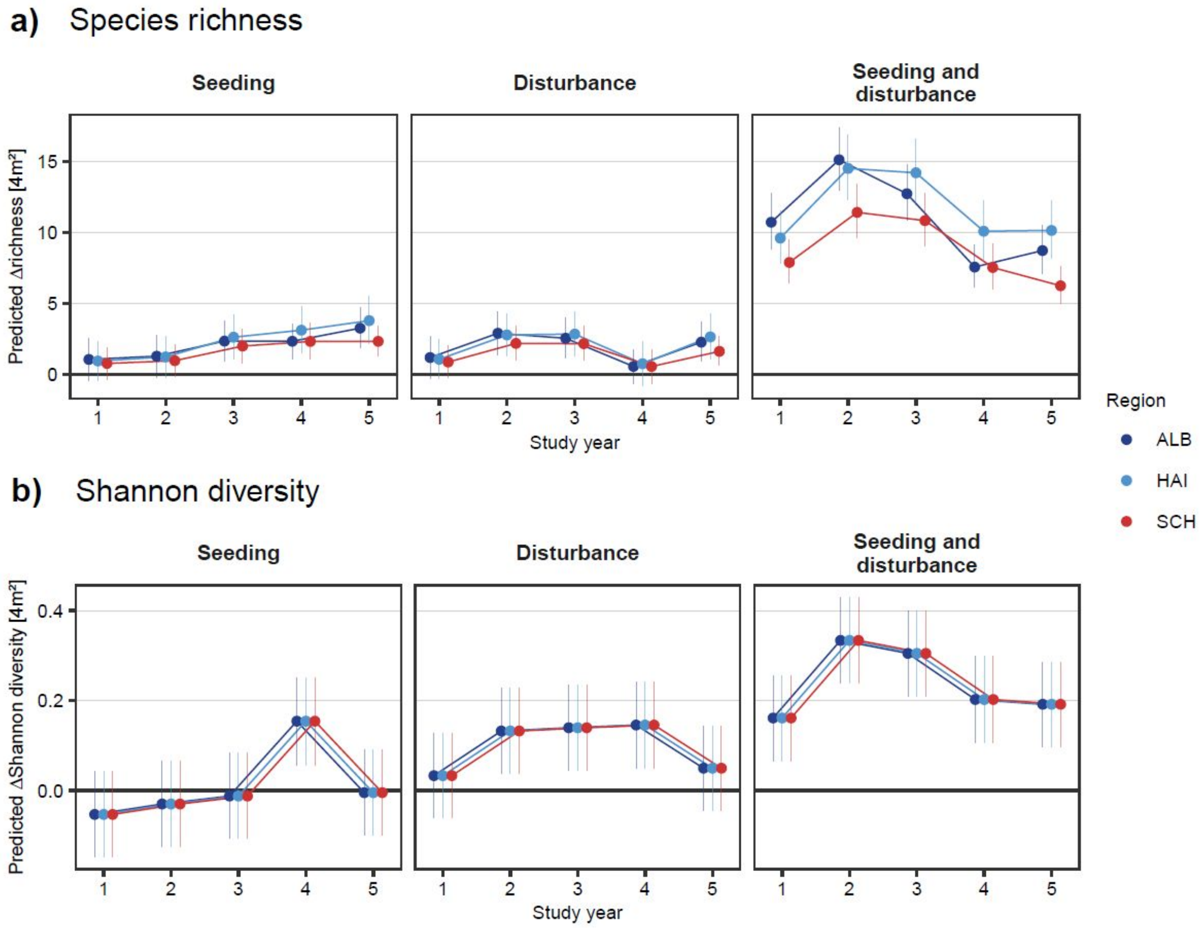

Figure 1: Predicted effects of seeding and soil disturbance on differences in species richness and Shannon diversity compared to the control in the three study regions. While seeding only led to small increases in Δrichness, the combination of seeding and disturbance had a strong positive effect on species richness and Shannon diversity. Points indicate the median and error bars denote the 90% credible interval. The group-level effects of region and year, but not grassland site, were considered in predicting the expected values. Differences between regions in Δrichness result from the varying intercept of region and year together with the log-link in Poisson regression, while ΔShannon diversity was modelled as Gaussian.

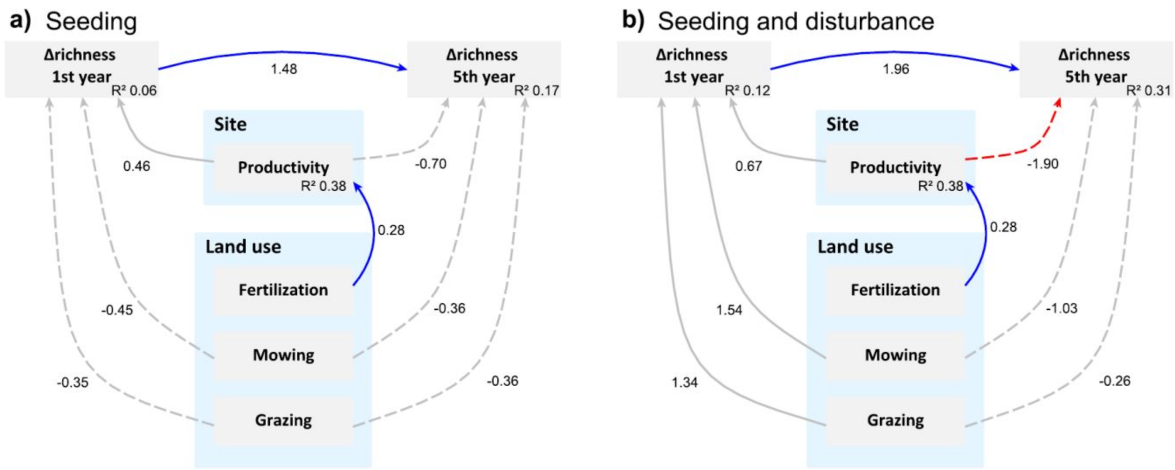

Figure 2: Direct and indirect land-use effects on Δrichness of a) the seeding only and b) the seeding and disturbance treatment. Explained variation of Δrichness in the first year and in the seeding treatment in general was low. In the combined treatment, land use had an indirect negative effect on Δrichness through a negative effect of productivity on Δrichness. Positive paths are shown as solid and negative paths as dashed lines along with standardized regression coefficients. Blue and red arrows indicate paths of which the 90% credible interval does not overlap zero, others are marked grey. Fixed effects of region are not shown but included in the Bayes R^2 (see Table 1 for details).

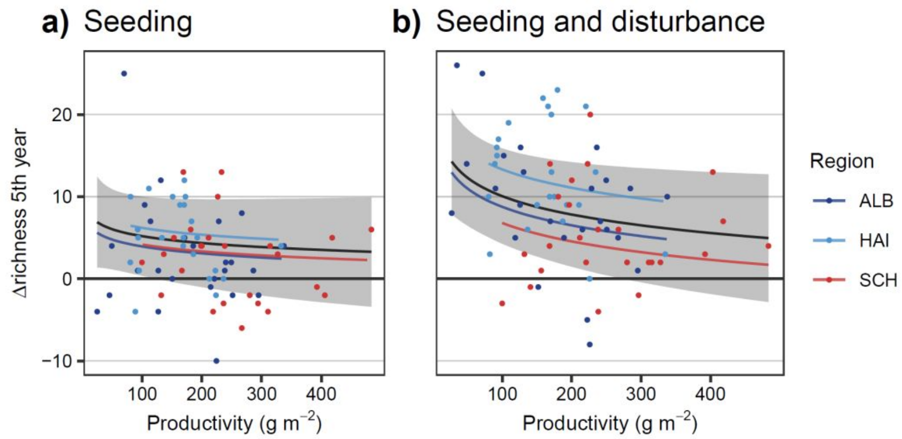

Figure 3: Conditional effect of productivity on Δrichness in the fifth year in a) the seeding only and b) the seeding and disturbance treatment. Overall Δrichness was lower and the effect of productivity weak in the seeding only treatment, but Δrichness declined with productivity on the combined treatment. Lines denote the median and 90% credible interval of predicted Δrichness across all 73 grasslands (grey) and within regions (coloured), conditioned on the mean of the other predictors (see Fig. 2, Table 1).

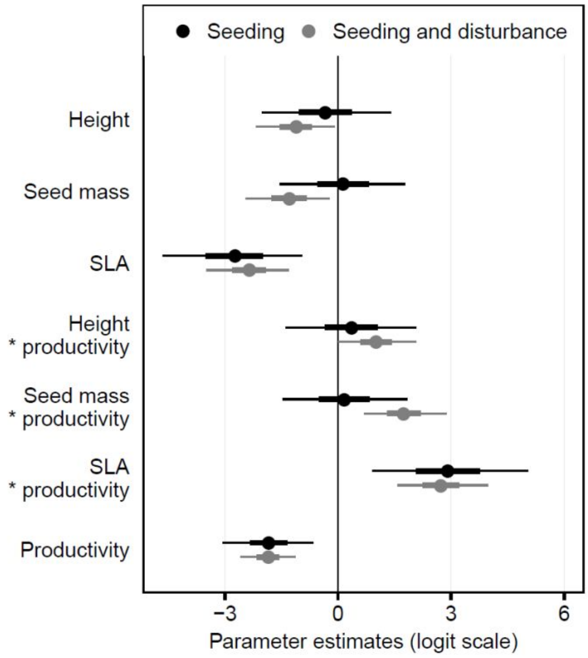

Figure 4: Posterior distributions of effects of traits, productivity and interactions on the establishment success of sown species on the seeding only (black) and seeding and disturbance treatment (grey). Traits considerably affected establishment, but effects varied with productivity. Establishment in the fifth year of the study was modelled with logistic regression and varying intercepts for sown species and grasslands. Points indicate the posterior median and lines show the 50% (thick line) and 90% credible interval (thin line). Height, seed mass and productivity were log-transformed, and all parameters scaled to unit standard deviation. See Table S2 (Appendix) for details.

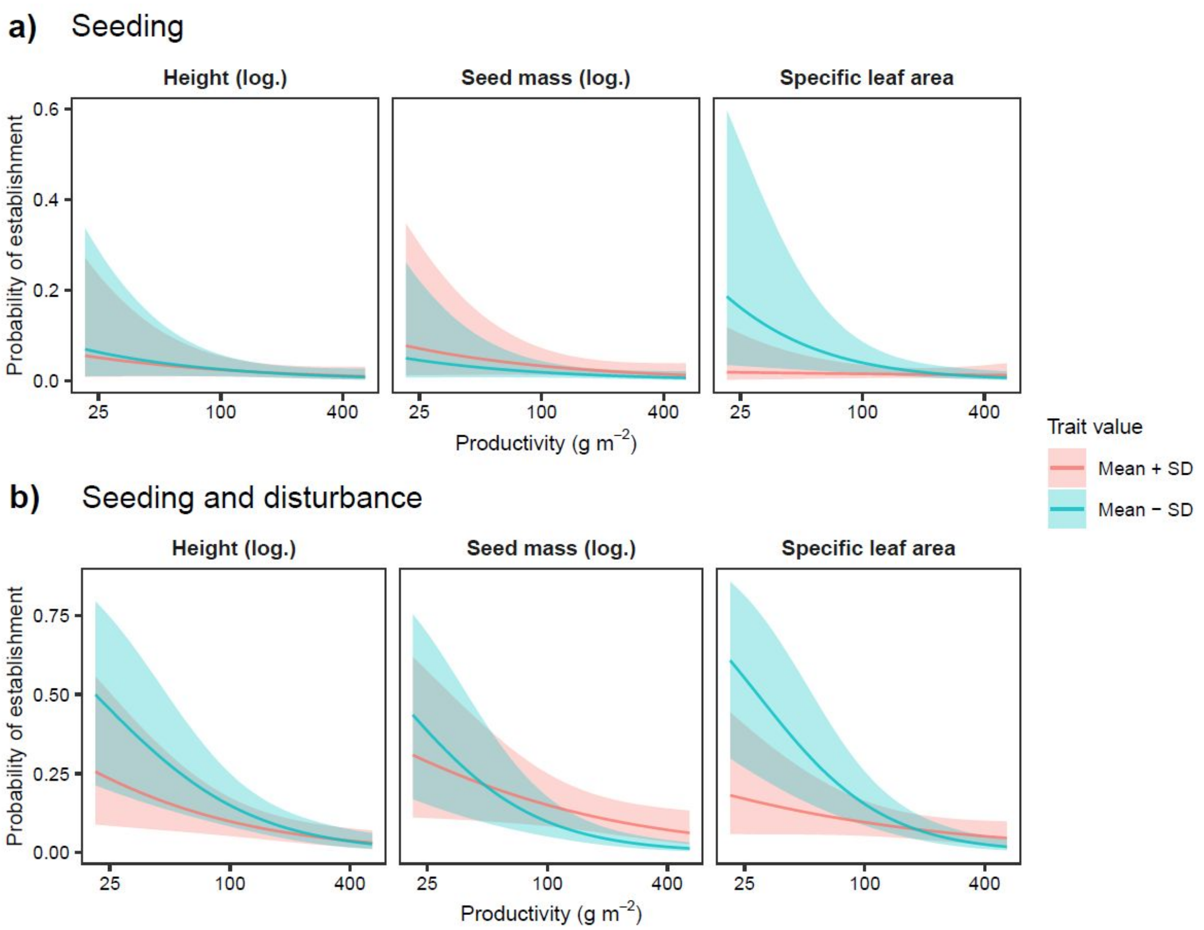

Figure 5: Conditional effects of high (mean plus one standard deviation SD, red) and low (mean minus one SD, blue) trait values along the productivity gradient (log-scale) on the establishment success of sown species on a) the seeding and b) the seeding and disturbance treatment. Especially in the combined treatment, trait effects on establishment considerably interacted with productivity. For each trait, lines denote the median and 90% credible interval of predicted establishment success, conditioned on the mean of the other respective traits (cf. Fig. 4, Table S2).

Table 1: Posterior distributions of direct and indirect land-use and region effects on Δrichness, i.e. the difference in plant species richness between the respective treatment and the control. Explained variation of Δrichness in the first year and in the seeding treatment in general was low. In the combined treatment, land use had an indirect negative effect on Δrichness through productivity. Intercepts of the Δrichness models refer to estimated means in the Alb region given average predictor values. 90% credible intervals that do not overlap zero are highlighted in bold. Productivity (biomass g m^{-2}) in both models was modelled as latent with measurement error σ.

	Seeding			**Seeding and disturbance**		
	Median	**5%**	**95%**	**Median**	**5%**	**95%**
Population-level effects						
Response: Δrichness 1st year						
Intercept (centered predictors, region ALB)	0.98	0.00	1.97	9.84	8.46	11.20
Region HAI	-0.20	-2.62	2.23	**-3.85**	**-7.17**	**-0.48**
Region SCH	-0.56	-3.21	2.10	-2.54	-6.15	1.09
Grazing (log-transformed)	-0.35	-1.96	1.28	1.34	-0.89	3.58
Mowing	-0.45	-2.16	1.30	1.54	-0.84	3.92
Productivity (log-transformed)	0.46	-0.92	1.80	0.67	-1.15	2.47
Response: Δrichness 5th year						
Intercept (centered predictors, region ALB)	3.29	2.25	4.34	8.80	7.55	10.04
Region HAI	2.29	-0.29	4.86	**4.56**	**1.39**	**7.71**
Region SCH	0.25	-2.57	3.09	-1.96	-5.34	1.42
Grazing (log-transformed)	-0.36	-2.10	1.38	-0.26	-2.34	1.80
Mowing	-0.36	-2.21	1.50	-1.03	-3.24	1.17
Productivity (log-transformed)	-0.70	-2.17	0.75	**-1.90**	**-3.54**	**-0.23**
Δrichness 1st year	**1.48**	**0.41**	**2.55**	**1.96**	**0.63**	**3.31**
Response: productivity (Gamma distribution, log-link)						
Intercept (zero fertilization, region ALB)	4.86	4.68	5.04	4.86	4.67	5.04
Region HAI	-0.09	-0.28	0.10	-0.09	-0.28	0.10
Region SCH	**0.53**	**0.34**	**0.71**	**0.53**	**0.35**	**0.72**
Log fertilization	**0.28**	**0.19**	**0.36**	**0.28**	**0.19**	**0.36**
Family-specific parameters						
σ Δrichness 1st year	5.05	4.41	5.87	7.08	6.17	8.22
σ Δrichness 5th year	5.40	4.70	6.29	6.48	5.64	7.55
ϕ productivity	5967.9	4128.4	8906.9	5968.7	4141.1	8915.6
Productivity measurement error						
σ productivity	85.68	80.39	91.48	85.65	80.42	91.47
Bayes R^2						
Δrichness 1st year	0.06	0.02	0.15	0.12	0.04	0.24
Δrichness 5th year	0.17	0.07	0.29	0.31	0.18	0.44
Productivity	0.38	0.23	0.52	0.38	0.23	0.52

Appendix to '*Restoration of permanent grasslands by seeding: assessing the limiting factors along land-use gradients*'

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CONTENT

ADDITIONAL METHODS: MODEL SPECIFICATION AND PRIOR CHOICES

Seeding and disturbance effects on plant diversity over time

Plant species richness

$Species\ richness_i \sim Poisson(\mu_i)$, with

$Log(\mu_i) = \alpha + \beta_1{*}Disturbance_i + \beta2{*}Seeding_i + \beta3{*}Year_i +$

$\beta_4{*}Disturbance_i{*}Seeding_i + \beta_5{*}Disturbance_i{*}Seeding_i{*}Year_i +$

$Grassland_{i,j} + RegionYear_{i,k}$

$Grassland_j \sim Normal(0, \sigma_{Grassland}),$

$RegionYear_k \sim Normal(0, \sigma_{RegionYear}),$

Priors:

$\alpha \sim Student\_t(\nu=3, \mu=3, \sigma=10)$

$\beta \sim Normal(\mu=0, \sigma=2)$

$\sigma_{Grassland} \sim Student\_t(\nu=3, \mu=0, \sigma=10)$, constrained to be positive

$\sigma_{RegionYear} \sim Student\_t(\nu=3, \mu=0, \sigma=10)$, constrained to be positive,

Where species richness$_i$ is the observed species richness in a treatment, disturbance$_i$ is a dummy variable for the disturbance treatment, seeding$_i$ is a dummy variable for the seeding treatment, year$_i$ represents four dummy variables for the four years of the study, grassland$_{i,j}$ is the grassland site grouping factor and RegionYear$_{i,k}$ is the region times year interaction grouping factor.

Shannon diversity

The Shannon diversity model was specified with exactly the same model structure and prior distributions as the species richness model, but with a Normal response distribution and residual σ:

$Shannon\ diversity_i \sim Normal(\mu_i, \sigma)$, with μ_i as in the species richness model

Priors as in the species richness model, but additionally

$\sigma_{Grassland} \sim Student\_t(\nu=3, \mu=0, \sigma=10)$

Direct and indirect effects of land use on enrichment effect, multivariate models

Δrichness 1st year

$\Delta richness\ 1st\ year_i \sim Normal(\mu_i, \sigma)$, with

$$\mu_i = \alpha + \beta_1{*}Log(Productivity_i) + \beta_2{*}Log(Grazing_i) + \beta_3{*}Mowing_i + \beta_4{*}Region_i$$

Priors:

$\alpha \sim Student\_t(\nu=3, \mu=0, \sigma=10)$

$\beta \sim Normal(\mu=0, \sigma=10)$

$\sigma \sim Cauchy(\mu=0, \sigma=10)$, constrained to be positive,

where Δrichness 1st $year_i$ is the absolute difference in species richness of the respective treatment compared to the control in the first year of this study at grassland site i, $productivity_i$ is the latent `true' productivity, $grazing_i$ is the mean grazing intensity (livestock unit*grazing days*ha^{-1}) in 2014-2018, $mowing_i$ is the mean mowing frequency in 2014-2018 and $region_i$ represents two dummy variables for the three regions.

Δrichness 5th year

$\Delta richness\ 5th\ year_i \sim Normal(\mu_i, \sigma)$, with

$$\mu_i = \alpha + \beta_1{*}Log(Productivity_i) + \beta_2{*}Log(Grazing_i) + \beta_3{*}Mowing_i + \beta_4{*}Region_i + \beta_5{*}\Delta richness\ 1st\ year_i$$

Priors:

$\alpha \sim Student\_t(\nu=3, \mu=0, \sigma=10)$

$\beta \sim Normal(\mu=0, \sigma=10)$

$\sigma \sim Cauchy(\mu=0, \sigma=10)$, constrained to be positive,

where Δrichness 5th $year_i$ is the absolute difference in species richness of the respective treatment compared to the control in the fifth year of this study at grassland site i, $productivity_i$ is the latent `true' productivity, $grazing_i$ is the mean grazing intensity (livestock unit*grazing days*ha^{-1}) in 2014-2018, $mowing_i$ is the mean mowing frequency in 2014-2018, $region_i$ represents two dummy variables for the three regions and Δrichness 1st $year_i$ is the absolute difference in species richness of the respective treatment compared to the control in the first year of this study.

Productivity

$Productivity_i \sim Gamma(\mu_i, \phi)$, with

$$Log(\mu_i) = \alpha + \beta_1 * Log(Fertilization_i + 1) + \beta_2 * Region_i$$

Priors:

$\alpha \sim Student\_t(\nu=3, \mu=0, \sigma=10)$

$\beta \sim Normal(\mu=0, \sigma=2)$

$1/\varphi \sim Gamma(\alpha=0.01, \beta=0.01)$,

where $productivity_i$ is the latent `true' productivity at grassland site i, $fertilization_i$ is the mean amount of fertilizer applied (kg N*ha^{-1}) in 2014-2018 and $region_i$ represents two dummy variables for the three regions.

Biomass with measurement error

$Biomass_i \sim Normal(productivity_i, \sigma)$,

Priors:

$Productivity_i \sim Normal(\mu=GrasslandMean_i, \sigma=GrasslandSD_i)$

$\sigma \sim Cauchy(\mu=0, \sigma=150)$, constrained to be positive,

where $Biomass_{i,j}$ is the harvested biomass (g*m^{-2}) on one square meter in grassland site i and year j and $productivity_i$ the latent `true' productivity of grassland site i with measurement error σ. $GrasslandMean_i$ and $GrasslandSD_i$ represent informed priors for $productivity_i$, derived as the arithmetic mean and standard deviation of the harvested biomass on grassland site i across the five years of this study.

Plant functional traits effects on establishment

Establishment of sown plant species after five years

$Establishment_i \sim Bernoulli(\mu_i)$, with

$log(\mu_i / 1\text{-}\mu_i) = \alpha + \beta_1{*}Height_{i,k} + \beta_2{*}SLA_{i,k} + \beta_3{*}Seed\ mass_{i,k} + \beta_4{*}Productivity_{i,j} +$
$\beta_5{*}Productivity_{i,j}{*}Height_{i,k} + \beta_6{*}Productivity_{i,j}{*}SLA_{i,k} +$
$\beta_7{*}Productivity_{i,j}{*}Seed\ mass_{i,k} + Grassland_{i,j} + Species_{i,k}$

$Grassland_j \sim Normal(\mu=0, \sigma_{Grassland})$,

$Species_k \sim Normal(\mu=0, \sigma_{Species})$,

Priors:

$\alpha \sim Student\_t(\nu=3, \mu=0, \sigma=10)$

$\beta \sim Normal\_t(\mu=0, \sigma=5)$

$\sigma_{Grassland} \sim Student\_t(\nu=3, \mu=0, \sigma=10)$, constrained to be positive

$\sigma_{Species} \sim Student\_t(\nu=3, \mu=0, \sigma=10)$, constrained to be positive,

where $Establishment_i$ is the binary establishment of a sown species in the respective grassland in year five, $Height_{i,k}$ is the log-tranformed canopy height (meter) of species k, $SLA_{i,k}$ is the specific leaf area ($mm^2{*}mg^{-1}$), Seed $mass_{i,k}$ is the log-transformed seed mass (mg), $productivity_i$ is the latent `true' productivity at grassland site j, $grassland_{i,j}$ is the grassland site grouping factor and $species_{i,k}$ is the sown species grouping factor.

ADDITIONAL METHODS: EFFECT OF REGION AND RESIDENT SPECIES RICHNESS ON ΔRICHNESS

As an independent measure of resident (untreated) species richness, we recorded plant species in 2019 on additional 4 m*4 m squares close to the experimental plots on all grasslands. To test how Δrichness relates to the resident species richness of the same site, we modelled Δrichness with Gaussian errors as a function of region and resident richness, which was log-transformed and scaled to unit SD. We specified weakly informative normal priors and default vague priors for the intercept.

Increased Δrichness was related to higher resident species richness in the fifth year in both, seeding only and seeding and disturbance, treatments (Fig. S1, Table S3). We observed the highest increases in species richness through seeding and disturbance in already species-rich grasslands, whereas some species-poor grasslands did not gain any new species from either treatment.

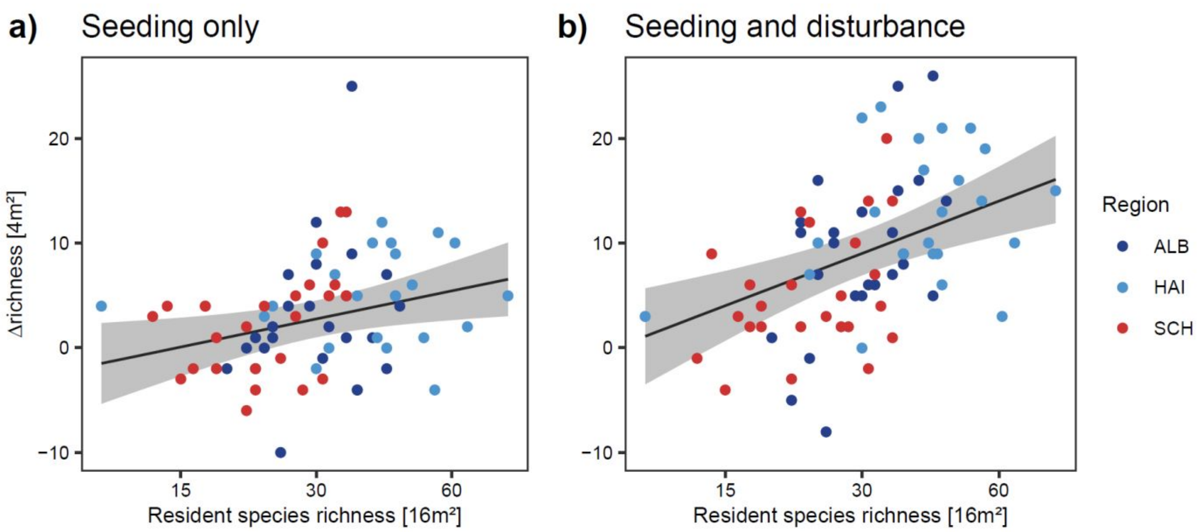


Figure S1: Conditional effect of resident species richness on Δrichness after five years in a) the seeding and b) the seeding and disturbance treatment. Lines refer to the predicted median and 90% credible intervals of Δrichness, conditioned on the region Alb (see Table 2 for details).

Table S1: Posterior distributions of main and interaction effects of seeding, disturbance and year on plant species richness and Shannon diversity in the 73 grasslands. Parameter effects are additive, i.e. the species richness on the seeding only treatment in year five is the sum of the intercept, the seeding main effect and the seeding times year five interaction. Note that species richness was modelled assuming Poisson errors with log-link, while the Shannon diversity was modelled as Gaussian. Despite, the effect sizes between both models are comparable because the Shannon diversity is the log of species richness weighted by the evenness (Spellerberg & Fedor, 2003).

	Species richness			**Shannon diversity**		
	Median	**5.0%**	**95.0%**	**Median**	**5.0%**	**95.0%**
Population-level effects						
Intercept (control in year one)	3.18	2.96	3.4	2.15	2.00	2.31
Disturbance	0.04	-0.01	0.10	0.03	-0.06	0.13
Disturbance*2nd year	0.06	-0.02	0.13	0.10	-0.03	0.23
Disturbance*3rd year	0.05	-0.02	0.13	0.11	-0.03	0.24
Disturbance*4th year	-0.02	-0.09	0.06	0.11	-0.02	0.25
Disturbance*5th year	0.05	-0.03	0.12	0.02	-0.12	0.15
Seeding	0.04	-0.02	0.09	-0.05	-0.15	0.04
Seeding*2nd year	0.01	-0.07	0.08	0.02	-0.11	0.16
Seeding*3rd year	0.05	-0.02	0.13	0.04	-0.09	0.18
Seeding*4th year	0.07	-0.01	0.14	0.21	0.07	0.34
Seeding*5th year	0.09	0.01	0.16	0.05	-0.08	0.18
Seeding*disturbance	0.25	0.18	0.32	0.18	0.05	0.31
Seeding*disturbance*2nd year	0.04	-0.06	0.14	0.05	-0.14	0.24
Seeding*disturbance*3rd year	-0.03	-0.13	0.07	0.00	-0.19	0.19
Seeding*disturbance*4th year	-0.07	-0.18	0.03	-0.28	-0.47	-0.09
Seeding*disturbance*5th year	-0.16	-0.26	-0.05	-0.03	-0.22	0.15
2nd year	0.04	-0.26	0.34	0.00	-0.19	0.20
3rd year	0.04	-0.26	0.34	0.01	-0.19	0.20
4th year	-0.02	-0.32	0.27	-0.17	-0.37	0.03
5th year	-0.05	-0.35	0.25	-0.20	-0.40	0.00
Group-level effects (varying intercepts)						
SD grassland (N=73)	0.33	0.28	0.38	0.37	0.32	0.42
SD region*year (N=15)	0.21	0.11	0.36	0.13	0.08	0.21
Family specific parameter σ				0.35	0.34	0.36
Bayes R^2						
conditional	0.86	0.85	0.87	0.57	0.55	0.58
marginal	0.16	0.10	0.28	0.09	0.05	0.15

Table S2: Posterior distributions of the effects of traits, productivity and interactions on the establishment success of sown species on the seeding only and seeding and disturbance treatment. Establishment in the fifth year of the experiment was modelled with logistic regression. Given here are the mean and the 90% credible interval of the posterior samples. The intercept refers to centred predictors, i.e. the average probability of establishment at average predictor values. All parameters but SLA were log-transformed and scaled to unit SD to compare effect sizes. Varying intercepts for species and grassland were included.

	Seeding			**Seeding and disturbance**		
	Median	**5 %**	**95 %**	**Median**	**5 %**	**95 %**
Population-level effects						
Intercept (centered predictors)	-4.06	-4.73	-3.48	-2.54	-3.01	-2.10
Height	-0.34	-2.01	1.41	-1.11	-2.18	-0.09
Seed mass	0.14	-1.54	1.79	-1.29	-2.45	-0.22
SLA	-2.73	-4.65	-0.95	-2.35	-3.49	-1.31
Productivity	-1.84	-3.06	-0.65	-1.85	-2.58	-1.13
Height * productivity	0.36	-1.39	2.07	1.01	0.00	2.07
Seed mass * productivity	0.17	-1.46	1.83	1.74	0.70	2.89
SLA * productivity	2.91	0.90	5.05	2.73	1.57	3.97
Group-level effects (varying intercepts)						
SD grassland (N=73)	1.81	1.43	2.3	1.35	1.11	1.66
SD species (N=73)	1.81	1.38	2.37	1.59	1.3	1.96
Bayes R^2						
conditional	0.46	0.28	0.50	0.41	0.37	0.43
marginal	0.17	0.01	0.38	0.22	0.08	0.29

Table S3: Posterior distributions of the effect of region and resident species richness on Δrichness. Δrichness in the fifth year was modelled as a function of region and resident species richness in the same year (log-transformed and scaled to unit SD).

	Seeding			Seeding and disturbance		
	Median	**5 %**	**95 %**	**Median**	**5 %**	**95 %**
Population-level effects						
Intercept (region ALB, centered predictors)	2.75	0.99	4.50	8.99	6.90	11.10
Region HAI	1.08	-1.60	3.76	1.56	-1.63	4.75
Region SCH	0.68	-1.93	3.30	-1.86	-4.99	1.24
Resident richness (log.)	3.87	0.72	6.98	7.21	3.50	10.90
Family Specific Parameters						
σ	5.4	0.47	4.72	6.44	0.56	5.63
Bayes R^2	0.11	0.03	0.22	0.28	0.15	0.39

Table S4: Overview of plant species sown and established in the seeding only treatment in the 73 grasslands in three regions. The number of grasslands a species was newly sown does not necessarily match the number of grasslands within a region because observations were omitted if a species was recorded in the control or disturbance treatment during the five years of the experiment. Sown species have successfully established if they were observed in the fifth year of the experiment.

	established	ALB		HAI		SCH	
		No. grasslands		No. grasslands		No. grasslands	
	%	sown	established	sown	established	sown	established
Non-legume herbs							
Achillea millefolium	33	7	1	5	3	-	-
Agrimonia eupatoria	8	17	1	7	2	25	1
Anthriscus sylvestris	3	8	0	12	1	20	0
Betonica officinalis	4	24	0	23	2	-	-
Campanula rotundifolia	0	16	0	23	0	25	0
Cardamine pratensis	10	20	2	-	-	-	-
Centaurea jacea	17	24	1	15	6	25	4
Centaurea scabiosa	8	25	0	23	3	25	3
Cichorium intybus	0	25	0	10	0	21	0
Cirsium oleraceum	2	22	1	23	0	21	0
Clinopodium vulgare	7	25	0	21	3	-	-
Crepis biennis	17	12	2	-	-	-	-
Daucus carota	7	18	0	6	2	18	1
Dianthus carthusianorum	17	24	3	22	5	-	-
Falcaria vulgaris	0	-	-	-	-	24	0
Galium mollugo	15	3	0	9	2	14	2
Geranium pratense	23	13	1	18	6	-	-
Heracleum sphondylium	7	10	0	18	2	18	1
Hypericum perforatum	5	19	1	16	1	23	1
Hypochaeris radicata	6	19	2	23	1	22	1
Knautia arvensis	10	16	4	-	-	24	0
Leontodon autumnalis	6	21	1	-	-	14	1
Leontodon hispidus	0	20	0	17	0	24	0
Leucanthemum vulgare	12	18	1	15	3	-	-
Linaria vulgaris	0	25	0	22	0	-	-
Lychnis flos-cuculi	1	24	0	22	0	24	1
Origanum vulgare	7	24	2	23	1	24	2
Pastinaca sativa	0	25	0	12	0	-	-
Pimpinella major	0	-	-	22	0	25	0
Pimpinella saxifraga	0	17	0	-	-	25	0
Plantago lanceolata	7	3	1	2	0	9	0
Plantago media	16	11	1	16	6	23	1
Primula veris	25	22	3	18	7	-	-
Prunella vulgaris	0	25	0	19	0	25	0
Ranunculus acris	0	3	0	13	0	-	-
Ranunculus bulbosus	21	14	3	-	-	-	-
Rumex acetosa	5	6	1	16	0	-	-
Rumex acetosella	0	-	-	-	-	20	0
Salvia pratensis	3	22	0	23	0	25	2
Sanguisorba minor	22	19	4	20	5	21	4
Sanguisorba officinalis	0	-	-	-	-	25	0
Scabiosa columbaria	2	-	-	22	0	23	1
Silaum silaus	0	25	0	-	-	24	0
Silene latifolia	1	25	0	23	0	20	1

Table S4 continued

	established	ALB		HAI		SCH	
		No. grasslands		No. grasslands		No. grasslands	
	%	sown	established	sown	established	sown	established
Non-legume herbs							
Silene vulgaris	3	23	0	23	1	25	1
Succisa pratensis	0	-	-	-	-	25	0
Thymus pulegioides	5	18	0	-	-	24	2
Tragopogon pratensis	12	16	1	11	5	22	0
Veronica chamaedrys	5	6	1	-	-	14	0
Veronica officinalis	0	25	0	-	-	-	-
Legumes							
Lathyrus pratensis	24	18	3	16	5	-	-
Lotus corniculatus	0	13	0	-	-	-	-
Medicago lupulina	0	14	0	-	-	-	-
Trifolium campestre	0	20	0	-	-	-	-
Trifolium medium	0	20	0	-	-	-	-
Trifolium pratense	29	1	0	6	2	-	-
Vicia cracca	22	18	4	-	-	-	-
Graminoids							
Agrostis capillaris	2	24	0	17	0	20	1
Anthoxanthum odoratum	3	10	0	20	1	-	-
Arrhenatherum elatius	16	7	0	4	1	14	3
Avenula pubescens	8	10	0	14	2	-	-
Briza media	2	21	1	20	0	-	-
Bromus erectus	0	15	0	19	0	-	-
Bromus hordeaceus	12	11	0	4	2	11	1
Cynosurus cristatus	7	8	0	13	3	21	0
Dactylis glomerata	29	2	0	1	1	4	1
Deschampsia cespitosa	2	25	0	-	-	21	1
Festuca pratensis	0	3	0	-	-	12	0
Festuca rubra	8	9	1	4	0	11	1
Holcus lanatus	11	-	-	-	-	9	1
Luzula campestris	10	18	1	19	3	23	2
Poa pratensis	100	2	2	-	-	-	-
Trisetum flavescens	6	3	0	7	2	22	0

Table S5: Overview of plant species sown and established in the seeding and disturbance treatment in the 73 grasslands in three regions. The number of grasslands a species was newly sown does not necessarily match the number of grasslands within a region because observations were omitted if a species was recorded in the control or disturbance treatment during the five years of the experiment. Sown species have successfully established if they were observed in the fifth year of the experiment.

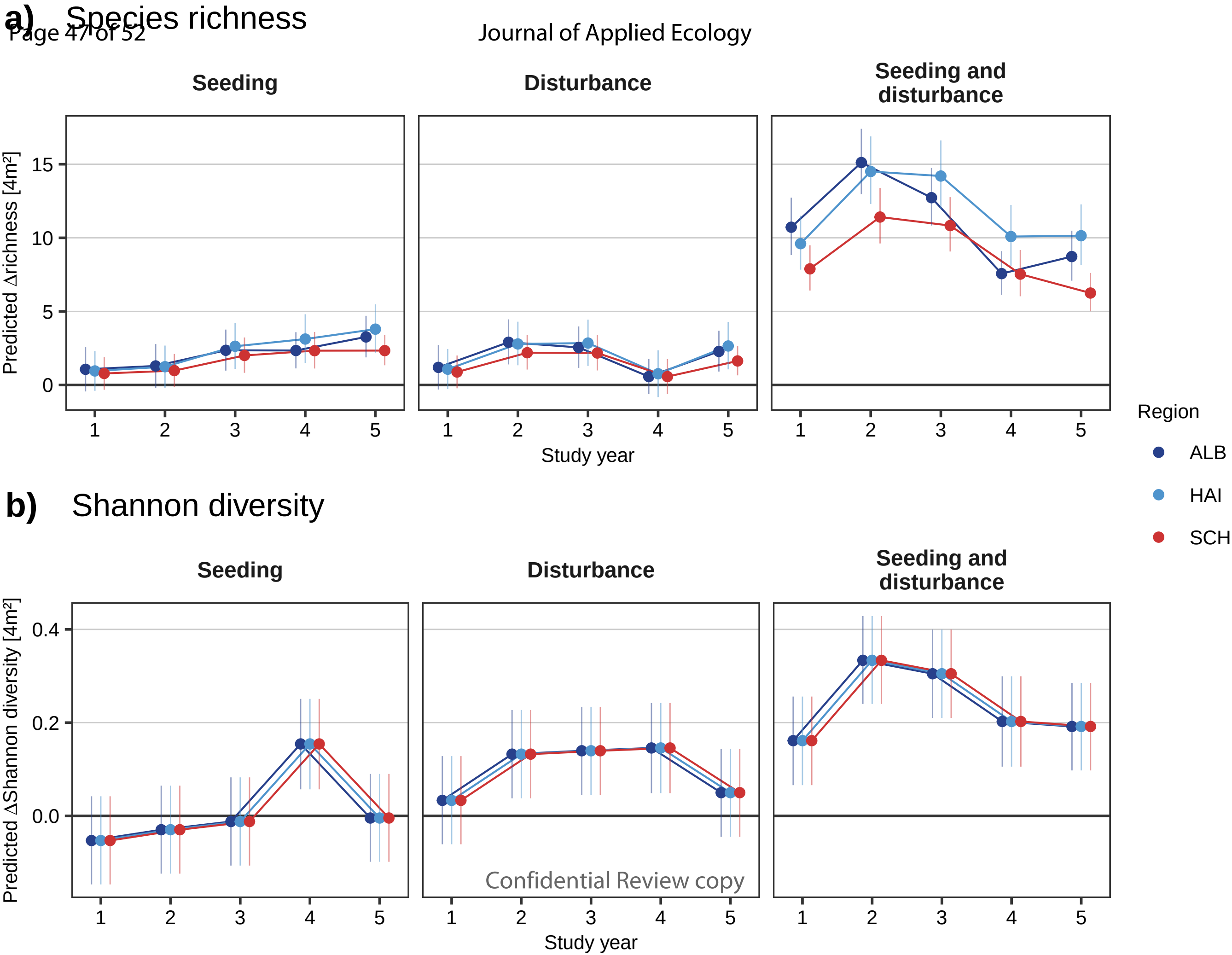
		ALB		HAI		SCH	
	established	No. grasslands		No. grasslands		No. grasslands	
	%	sown	established	sown	established	sown	established
Non-legume herbs							
Achillea millefolium	67	7	6	5	2	-	-
Agrimonia eupatoria	8	17	2	7	2	25	0
Anthriscus sylvestris	0	8	0	12	0	20	0
Betonica officinalis	17	24	4	23	4	-	-
Campanula rotundifolia	0	16	0	23	0	25	0
Cardamine pratensis	5	20	1	-	-	-	-
Centaurea jacea	22	24	3	15	10	25	1
Centaurea scabiosa	25	25	4	23	9	25	5
Cichorium intybus	5	25	0	10	1	21	2
Cirsium oleraceum	2	22	1	23	0	21	0
Clinopodium vulgare	20	25	0	21	9	-	-
Crepis biennis	42	12	5	-	-	-	-
Daucus carota	12	18	2	6	1	18	2
Dianthus carthusianorum	43	24	10	22	10	-	-
Falcaria vulgaris	0	-	-	-	-	24	0
Galium mollugo	50	3	2	9	5	14	6
Geranium pratense	61	13	6	18	13	-	-
Heracleum sphondylium	17	10	0	18	1	18	7
Hypericum perforatum	9	19	3	16	0	23	2
Hypochaeris radicata	16	19	6	23	2	22	2
Knautia arvensis	20	16	8	-	-	24	0
Leontodon autumnalis	23	21	5	-	-	14	3
Leontodon hispidus	7	20	2	17	2	24	0
Leucanthemum vulgare	21	18	4	15	3	-	-
Linaria vulgaris	17	25	5	22	3	-	-
Lychnis flos-cuculi	4	24	0	22	3	24	0
Origanum vulgare	15	24	8	23	0	24	3
Pastinaca sativa	8	25	2	12	1	-	-
Pimpinella major	0	-	-	22	0	25	0
Pimpinella saxifraga	2	17	0	-	-	25	1
Plantago lanceolata	21	3	2	2	0	9	1
Plantago media	22	11	2	16	8	23	1
Primula veris	28	22	4	18	7	-	-
Prunella vulgaris	6	25	0	19	3	25	1
Ranunculus acris	6	3	0	13	1	-	-
Ranunculus bulbosus	14	14	2	-	-	-	-
Rumex acetosa	41	6	1	16	8	-	-
Rumex acetosella	5	-	-	-	-	20	1
Salvia pratensis	1	22	0	23	0	25	1
Sanguisorba minor	32	19	5	20	11	21	3
Sanguisorba officinalis	0	-	-	-	-	25	0
Scabiosa columbaria	4	-	-	22	0	23	2
Silaum silaus	0	25	0	-	-	24	0
Silene latifolia	9	25	1	23	2	20	3

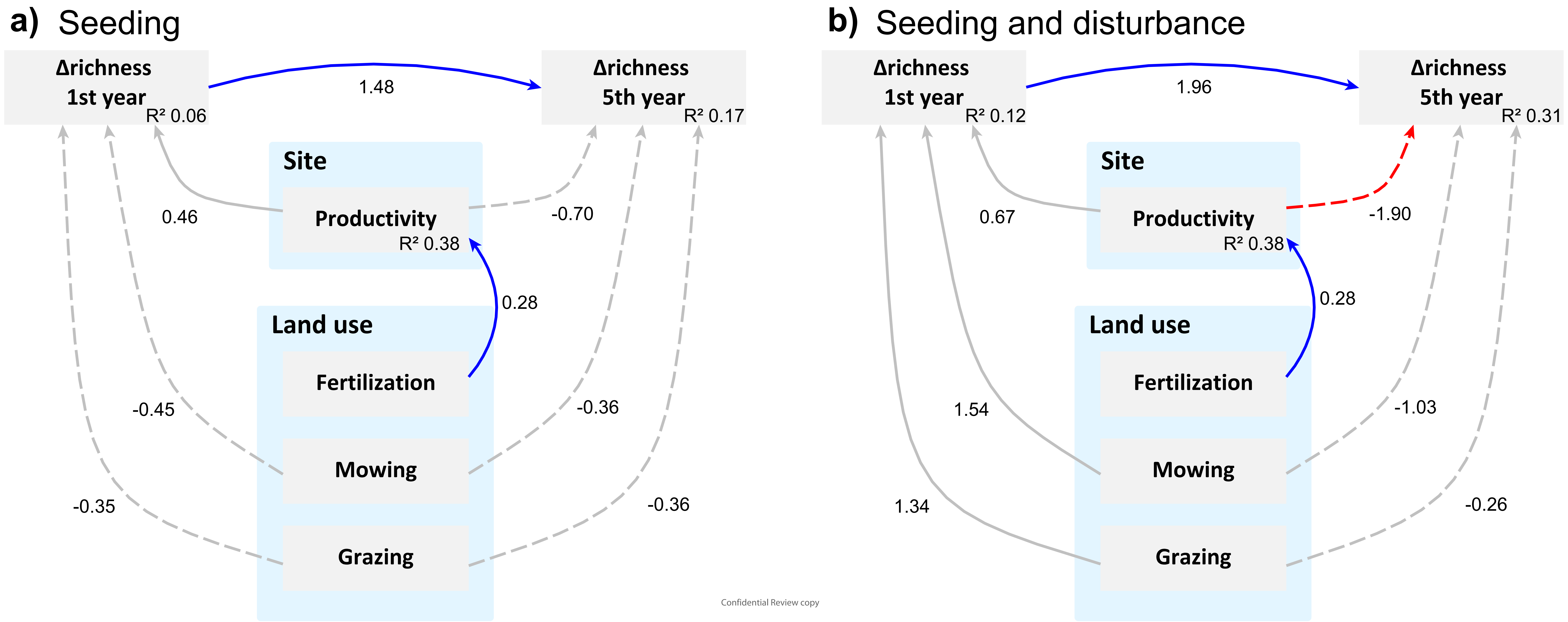
Table S5 continued

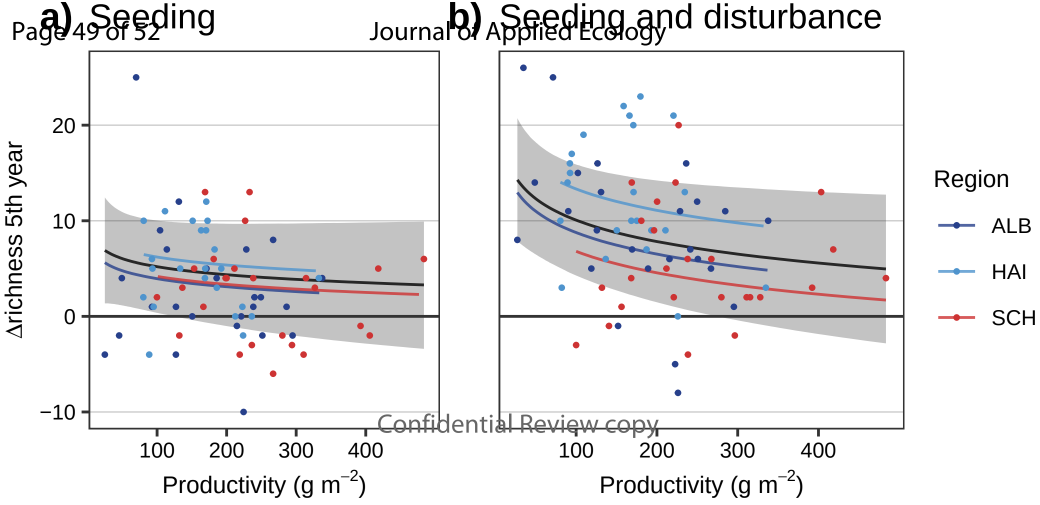
		ALB		HAI		SCH	
	established	No. grasslands		No. grasslands		No. grasslands	
	%	sown	established	sown	established	sown	established
Non-legume herbs							
Silene vulgaris	34	23	3	23	16	25	5
Succisa pratensis	0	-	-	-	-	25	0
Thymus pulegioides	10	18	1	-	-	24	3
Tragopogon pratensis	8	16	0	11	4	22	0
Veronica chamaedrys	10	6	1	-	-	14	1
Veronica officinalis	8	25	2	-	-	-	-
Legumes							
Lathyrus pratensis	59	18	8	16	12	-	-
Lotus corniculatus	8	13	1	-	-	-	-
Medicago lupulina	7	14	1	-	-	-	-
Trifolium campestre	0	20	0	-	-	-	-
Trifolium medium	0	20	0	-	-	-	-
Trifolium pratense	43	1	0	6	3	-	-
Vicia cracca	44	18	8	-	-	-	-
Graminoids							
Agrostis capillaris	0	24	0	17	0	20	0
Anthoxanthum odoratum	20	10	1	20	5	-	-
Arrhenatherum elatius	20	7	2	4	2	14	1
Avenula pubescens	29	10	0	14	7	-	-
Briza media	27	21	4	20	7	-	-
Bromus erectus	29	15	6	19	4	-	-
Bromus hordeaceus	31	11	1	4	3	11	4
Cynosurus cristatus	5	8	0	13	2	21	0
Dactylis glomerata	57	2	2	1	1	4	1
Deschampsia cespitosa	4	25	0	-	-	21	2
Festuca pratensis	7	3	0	-	-	12	1
Festuca rubra	13	9	2	4	0	11	1
Holcus lanatus	22	-	-	-	-	9	2
Luzula campestris	13	18	4	19	3	23	1
Poa pratensis	50	2	1	-	-	-	-
Trisetum flavescens	9	3	1	7	1	22	1

REFERENCES

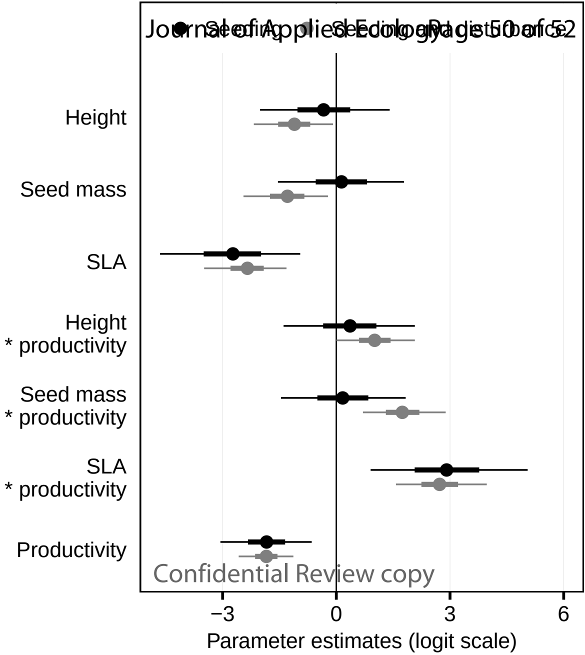
Spellerberg, I. F., & Fedor, P. J. (2003). A tribute to Claude Shannon (1916-2001) and a plea for more rigorous use of species richness, species diversity and the ‘Shannon-Wiener’ Index. *Global Ecology and Biogeography*, *12*(3), 177–179. https://doi.org/10.1046/j.1466-822X.2003.00015.x

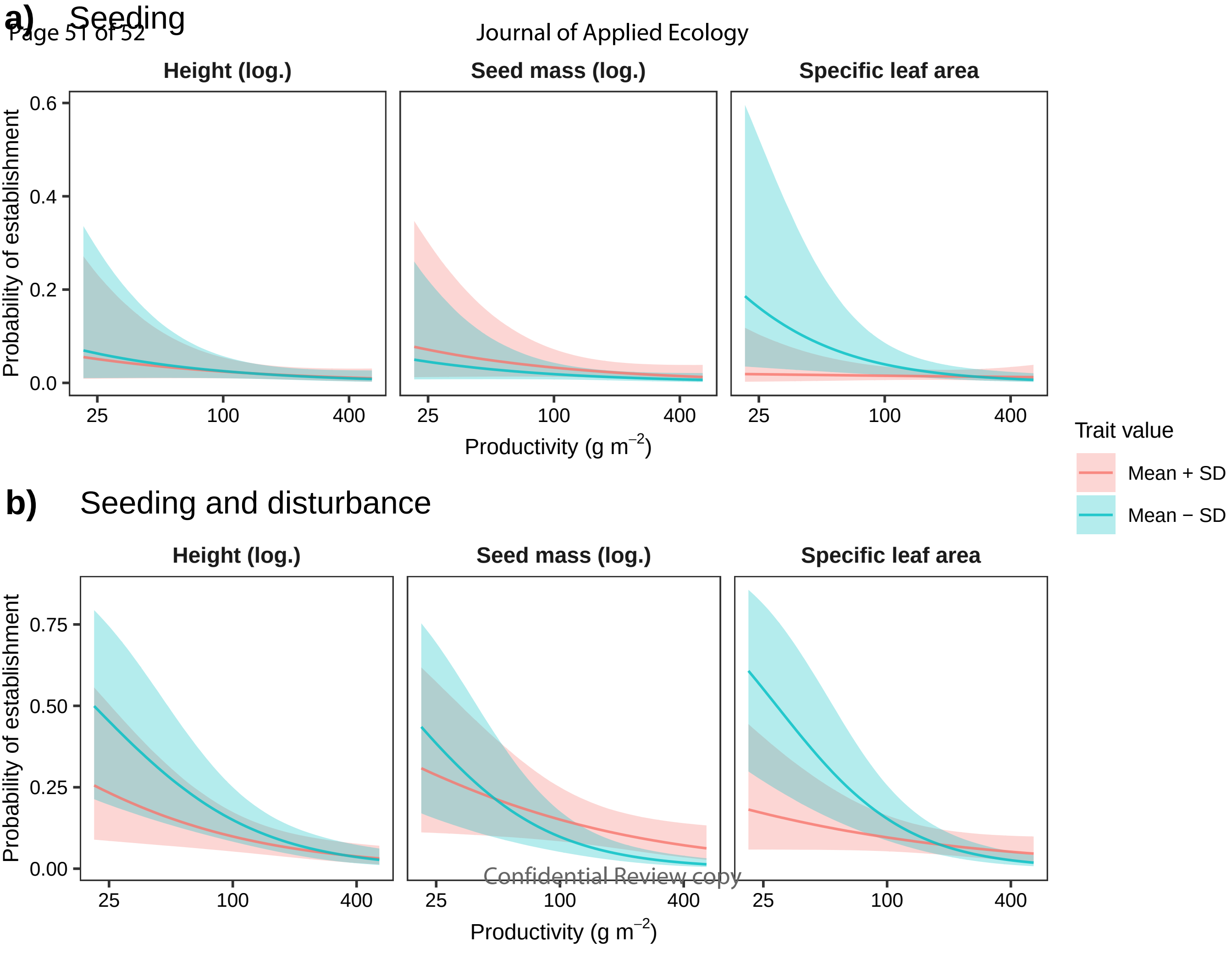

a) Species richness
Seeding
Disturbance
Seeding and disturbance
Predicted Δrichness [4m²]
0
5
10
15
1
2
3
4
5
Study year
Region
ALB
HAI
SCH
b) Shannon diversity
Seeding
Disturbance
Seeding and disturbance
Predicted ΔShannon diversity [4m²]
0.0
0.2
0.4
Study year


a) Seeding
Δrichness 1st year
R² 0.06
Δrichness 5th year
R² 0.17
1.48
Site
Productivity
R² 0.38
0.46
-0.70
0.28
Land use
Fertilization
Mowing
Grazing
-0.45
-0.36
-0.35
-0.36
b) Seeding and disturbance
Δrichness 1st year
R² 0.12
Δrichness 5th year
R² 0.31
1.96
Site
Productivity
R² 0.38
0.67
-1.90
0.28
Land use
Fertilization
Mowing
Grazing
1.54
-1.03
1.34
-0.26



a) Seeding
b) Seeding and disturbance
Δrichness 5th year
20
10
0
−10
100
200
300
400
Productivity (g m^{-2})
Region
ALB
HAI
SCH


Seeding
Seeding and disturbance
Height
Seed mass
SLA
Height
* productivity
Seed mass
* productivity
SLA
* productivity
Productivity
−3
0
3
6
Parameter estimates (logit scale)


a) Seeding
Height (log.)
Seed mass (log.)
Specific leaf area
Probability of establishment
0.0
0.2
0.4
0.6
25
100
400
Productivity (g m−2)
Trait value
Mean + SD
Mean − SD
b) Seeding and disturbance
Height (log.)
Seed mass (log.)
Specific leaf area
Probability of establishment
0.00
0.25
0.50
0.75
25
100
400
Productivity (g m−2)

	Seeding			Seeding and disturbance		
	Median	**5%**	**95%**	**Median**	**5%**	**95%**
Population-level effects						
Response: Δrichness 1st year						
Intercept (centered predictors, region ALB)	0.98	0.00	1.97	9.84	8.46	11.20
Region HAI	-0.20	-2.62	2.23	**-3.85**	**-7.17**	**-0.48**
Region SCH	-0.56	-3.21	2.10	-2.54	-6.15	1.09
Grazing (log-transformed)	-0.35	-1.96	1.28	1.34	-0.89	3.58
Mowing	-0.45	-2.16	1.30	1.54	-0.84	3.92
Productivity (log-transformed)	0.46	-0.92	1.80	0.67	-1.15	2.47
Response: Δrichness 5th year						
Intercept (centered predictors, region ALB)	3.29	2.25	4.34	8.80	7.55	10.04
Region HAI	2.29	-0.29	4.86	**4.56**	**1.39**	**7.71**
Region SCH	0.25	-2.57	3.09	-1.96	-5.34	1.42
Grazing (log-transformed)	-0.36	-2.10	1.38	-0.26	-2.34	1.80
Mowing	-0.36	-2.21	1.50	-1.03	-3.24	1.17
Productivity (log-transformed)	-0.70	-2.17	0.75	**-1.90**	**-3.54**	**-0.23**
Δrichness 1st year	**1.48**	**0.41**	**2.55**	**1.96**	**0.63**	**3.31**
Response: productivity (Gamma distribution, log-link)						
Intercept (zero fertilization, region ALB)	4.86	4.68	5.04	4.86	4.67	5.04
Region HAI	-0.09	-0.28	0.10	-0.09	-0.28	0.10
Region SCH	**0.53**	**0.34**	**0.71**	**0.53**	**0.35**	**0.72**
Log fertilization	**0.28**	**0.19**	**0.36**	**0.28**	**0.19**	**0.36**
Family-specific parameters						
σ Δrichness 1st year	5.05	4.41	5.87	7.08	6.17	8.22
σ Δrichness 5th year	5.40	4.70	6.29	6.48	5.64	7.55
ϕ productivity	5967.9	4128.4	8906.9	5968.7	4141.1	8915.6
Productivity measurement error						
σ productivity	85.68	80.39	91.48	85.65	80.42	91.47
Bayes R^2						
Δrichness 1st year	0.06	0.02	0.15	0.12	0.04	0.24
Δrichness 5th year	0.17	0.07	0.29	0.31	0.18	0.44
Productivity	0.38	0.23	0.52	0.38	0.23	0.52