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Restoration of plant diversity in permanent grassland by seeding: assessing the limiting factors along land-use gradients

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1 **Restoration of plant diversity in permanent grassland by seeding:**
2 **assessing the limiting factors along land-use gradients**

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16 **Keywords:** dispersal limitation, fertilization, functional traits, land-use intensity, productivity, seed
17 addition, seedling establishment, trait-environment interactions

18 ABSTRACT

- 19 1. In the past decades, land-use intensification has caused dramatic declines in grassland biodiversity,
20 and in Europe this decline has not yet been halted. Therefore, a major challenge in ecological
21 restoration is to effectively restore plant diversity in permanent grasslands. As species richness is
22 often limited by seed dispersal, introducing locally absent species is crucial. Dispersal limitation can
23 potentially be overcome by seeding diverse seed mixtures, but restoration outcomes are highly
24 variable. It remains poorly understood how land-use intensity constrains restoration and how to
25 consider plant functional traits to increase restoration success.
- 26 2. We established a full-factorial experiment with high-diversity seeding and topsoil disturbance in 73
27 grasslands along land-use intensity and productivity gradients and evaluated the restoration
28 success over five years. In addition, after five years we assessed the number of established species
29 and tested whether specific traits promoted the establishment of sown species in interaction with
30 productivity.
- 31 3. Plant diversity increased considerably when seeding and disturbance were combined, while
32 seeding alone only slightly increased species richness. We found no direct effect of land-use
33 intensity on the establishment of sown species, but fertilization indirectly limited establishment in
34 the combined treatment via a negative effect of productivity.
- 35 4. Functional traits structured the establishment of sown species, especially in the combined
36 treatments, but effects varied with productivity. Species with low seed mass and low specific leaf
37 area had greater establishment success in low-productivity grasslands, whereas species with high
38 seed mass had greater establishment in high-productivity grasslands.
- 39 5. *Synthesis and applications* Our results highlight the potential of using diverse seed mixtures for
40 biodiversity restoration in a wide range of permanent grasslands, especially when combined with

41 soil disturbance. However, productivity both limited restoration success and affected
42 establishment via an interaction with plant functional traits. As productivity is a major constraint in
43 grassland restoration, we strongly recommend to first stop fertilization and reduce soil nutrient
44 loads in highly productive grasslands. Restoration by seeding, with or without disturbance, should
45 only be applied when the productivity is reduced, and the local environment should be considered
46 to compile site-specific seed mixtures to maximise restoration success.

47 INTRODUCTION

48 Land-use intensification has dramatically impacted both biodiversity and ecosystem service provision of
49 permanent grasslands (IPBES, 2019; Newbold et al., 2016). Europe, for example, faced alarming declines
50 in grassland areas and deteriorations in conservation status, and these effects have not yet been halted
51 by agri-environmental schemes (Janssen et al., 2016). Severe declines in plant species richness have
52 been especially caused by intensive fertilization (Gross et al., 2009; Socher et al., 2012), such that even
53 common plant species have decreased in abundance at alarming rates (Jansen et al., 2019). Grasslands
54 therefore are a major target of ecological restoration (Blakesley & Buckley, 2016). Yet, our predictions of
55 restoration success are often inaccurate because outcomes vary greatly among restoration efforts,
56 mostly because of widespread variability in restoration approaches and site conditions (Brudvig et al.,
57 2017).

58 To restore the local plant species richness in grasslands, seed dispersal limitation must be overcome
59 (Clark et al., 2007; Münzbergová & Herben, 2005; Myers & Harms, 2009). Most grassland species are
60 short-distance seed dispersers (Coulson et al., 2001; Sperry et al., 2019) and do not form persistent soil
61 seed banks (Kiss et al., 2018). Therefore, a mandatory step to restore plant species richness is to actively
62 introduce locally absent species. One widely applied measure to restore vegetation with a specific
63 taxonomic composition is hay transfer (Bischoff et al., 2018; Kiehl et al., 2010), but this practice is often
64 constrained by appropriate donor sites or low transfer rates of species with particular early or late
65 phenology (Wagner, Hulmes, Hulmes, Redhead, et al., 2020). Hay transfer can be supplemented or
66 replaced by commercially available seeds of regional provenance, as diverse seeding enables one to
67 tailor the species composition to a target community (Baasch et al., 2016). In addition, diverse seeding
68 could be implemented in agricultural routines to increase diversity at larger scales. Restoration by
69 seeding has been successfully applied on ex-arable land (Pywell et al., 2002; Wagner, Hulmes, Hulmes,

70 Nowakowski, et al., 2020) and in low- and high-productivity grasslands (Ladouceur et al., 2020; Pywell et
71 al., 2007; Zobel et al., 2000). Yet, most studies considered single or few sites, which makes it difficult to
72 assess the significance of key constraining factors across real world gradients of land-use intensity and
73 productivity.

74 In the germination and seedling stages of a plant, safe microsites such as gaps within the established
75 vegetation are crucial (Grubb, 1977). These gaps in the established sward are often created via topsoil
76 disturbance, which enables seed-soil contact and amplifies seed germination through reduced
77 competition and increased light availability at the soil surface (Bischoff et al., 2018; Myers & Harms,
78 2009). Such microsites create a safe regeneration space even in productive grasslands (Foster et al.,
79 2004), but competition with the regrowing vegetation sward in the years after disturbance may impede
80 long-term establishment in productive sites (Dickson & Foster, 2008). This competition for light can be
81 reduced with repeated biomass removal through mowing or grazing, thereby increasing the
82 establishment success (Dickson & Foster, 2008). Additionally, grazing creates microsites by trampling,
83 which could further facilitate establishment (Kladivová & Münzbergová, 2016). Although high-diversity
84 seed mixtures increased diversity even in the long run (e.g. Maccherini & Santi, 2012), it remains largely
85 unclear how disturbance interacts with grazing or mowing to shape establishment in managed
86 grasslands. Determining how topsoil disturbance, grazing and mowing affect the long-term
87 establishment of seeds along productivity gradients can improve outcome predictions and may provide
88 guidance on how to prioritize sites for restoration actions.

89 To improve restoration success and maximise ecosystem functions, plant functional traits can help to
90 compile targeted seed mixtures (Laughlin, 2014). Because traits, especially canopy height, specific leaf
91 area and seed mass, represent fundamental trade-offs of plant strategies in response to the
92 environment and affect competitive and reproductive abilities (Westoby, 1998), they can be used, for

93 example, to select potentially successful species to increase restoration success (Pywell et al., 2003).
94 Further, a deeper understanding of assembly mechanisms in restoration enables us to restore
95 communities targeted to specific environmental conditions (Laughlin, 2014; Török & Helm, 2017).
96 Assembly mechanisms such as environmental filtering influence restoration success because it
97 structures the establishment of species with particular traits (Balazs et al., 2020; Zirbel & Brudvig, 2020).
98 Knowledge on how traits interact with environmental gradients, such as productivity and land-use
99 intensity, can assist in the selection of species based on local site conditions.

100 Here, we aimed to assess the long-term restoration success using a diverse and regionally adapted seed
101 mixture along gradients of land-use intensity and productivity, with and without prior topsoil
102 disturbance. We established a full-factorial experiment in 73 grasslands ranging from low-productivity
103 sheep pastures and single-cut meadows to highly fertilized meadows and mown pastures with four cuts
104 per year or intensive grazing. Short-term results from this experiment showed that intensively used,
105 species-poor grasslands increased strongly in species richness when seeding and topsoil disturbance
106 were combined, while seeding alone had no effect on diversity (Klaus et al., 2017). Here, we assessed
107 how land use, productivity and plant functional traits structure the long-term establishment of sown
108 species. Specifically, we investigate i) the effectiveness of seeding, disturbance and their combination to
109 enhance plant diversity over time, ii) the degree to which land-use intensity and productivity constrain
110 the establishment of sown species and iii) how traits, trait-environment and trait-management
111 interactions affect the establishment of sown species during restoration.

112

113 METHODS**114 *Study design***

115 We analysed five years of a seeding and disturbance experiment in 73 grasslands as part of the
116 Biodiversity Exploratories project (Fischer et al., 2010). We installed the experiment in three German
117 regions that span gradients in soil characteristics, elevation and climate that are representative of large
118 parts of Central Europe. The regions comprise i) the calcareous mid-mountain range Biosphere Reserve
119 Schwäbische Alb (48.4°N, 9.4°E), ii) the calcareous low-mountain range National Park Hainich-Dün and
120 surroundings (51.1°N, 10.4°E) and iii) the postglacial landscape of Biosphere Reserve Schorfheide-Chorin
121 (53.0°N, 14.0°E). While grasslands in the Schwäbische Alb and Hainich-Dün are restricted to mineral
122 soils, grasslands in Schorfheide-Chorin are situated on drained fen soils or slightly acidic sandy soils
123 (Fischer et al., 2010). Within each region, we selected 23–25 permanent grasslands along gradients of
124 land-use intensity, productivity and corresponding plant diversity, ranging from unfertilized sheep
125 pastures with 70 species per 16 m² to highly fertilized, productive and frequently mown grasslands with
126 10 species per 16 m² (Socher et al., 2012). To quantify land-use intensity, farmers were interviewed each
127 year to inquire on the amount of fertilizer used (in kg N ha⁻¹), mowing frequency per year and grazing
128 intensity (livestock unit × grazing days ha⁻¹) (Vogt et al., 2019). Here, we used averaged fertilization,
129 mowing and grazing intensities from 2014 to 2018.

130 We established a 2 × 2 factorial experiment with seeding and topsoil disturbance in 73 grasslands. This
131 resulted in four 7 m × 7 m treatments (control, seeding only, seeding and disturbance, disturbance only),
132 which we arranged in a rectangle with 2 m distance between treatments (see appendix S1). In October
133 2014, we applied the disturbance treatment by mechanical perturbation of the established sward and
134 the topsoil down to 10 cm with a rotary harrow or a rotary cultivator. The topsoil disturbance created a
135 high proportion of bare ground (~50% in the following spring; Schäfer et al., 2019) and was similar to

136 common agricultural re-seeding practices. We did not remove root and shoot fragments of the
137 disturbed sward so that plants could possibly regrow. See Klaus et al. (2017) for further details on the
138 experimental design.

139 For the seeding treatments, we used commercially available regional seed mixtures from certified seed
140 producers, composed of genotypes that are assumed to be adapted to regional environmental
141 conditions (Bucharova et al., 2017). The mixtures consisted of common and less-common species,
142 selected from the species pools of each individual region (Fischer et al., 2010) and included grasses,
143 legumes and forbs. Seeding density per species depended inversely on seed mass (high: 100 seeds m⁻² if
144 seed mass < 1 mg, medium: 34 seeds m⁻² between 1 mg and 10 mg, low: 17 seeds m⁻² > 10 mg). Two-
145 thirds of the mixture were sown in November 2014 and one-third in March 2015. In total, we sowed
146 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
147 and 47 species in Schorfheide-Chorin (no regional seeds of legumes available from seed producers for
148 this region).

149 We surveyed vegetation and measured productivity from 2015 to 2019 annually in May before the first
150 mowing or grazing took place. On all four 7 m × 7 m treatments in each of the 73 grasslands, we
151 recorded all vascular plant species on 2 m × 2 m quadrats and estimated percentage cover. As a
152 measure of competition, annually we clipped all living plant biomass on one square meter on the control
153 treatment (four 0.25 m² squares, different but close-by locations each year, see appendix S1). We dried
154 the biomass for 48 h at 80 °C and weighed it to the nearest gram. In 2018, we could not access three
155 grasslands due to early land use (i.e. missing data for 12 observations). In total, we recorded 1448
156 observations over the five years.

157 **Analysis**

158 *Seeding and disturbance effects on plant diversity*

159 We analysed how seeding and disturbance influenced plant diversity over time. We used two
160 complementary diversity indices, namely species richness and effective number of species S_{PIE} , which
161 accounts for community evenness by weighing abundant species more than rare species. We calculated
162 evenness as the probability of interspecific encounter $PIE = \sum_{i=1}^S p_i^2$, where S is species richness and p_i
163 is the relative cover of species i , and transformed PIE into an effective number of species $S_{PIE} = \frac{1}{1 - PIE}$
164 ([Chase et al., 2018](#); [Jost, 2006](#)). S_{PIE} equals species richness when all species have equal abundance, but
165 S_{PIE} decreases when cover is more unevenly distributed across species. We modelled species richness
166 and S_{PIE} as a function of seeding, disturbance and year, including all their interactions, and assumed
167 Poisson error structure for species richness and Gamma error structure for S_{PIE} , both with log link. We
168 treated year as categorical because effects over time were non-linear. We included varying intercepts
169 for grassland site to account for the experimental design and varying intercepts for year within region
170 (five years times three regions) because weather conditions and observers varied between years and
171 regions. The multi-level models were estimated in a hierarchical Bayesian framework using the Stan
172 probabilistic language ([Stan Development Team, 2020](#)) accessed via the package *brms* v2.14.4 ([Bürkner,](#)
173 [2017](#)) in R v4.0.3 ([R Core Team, 2020](#)). For all models, we specified weakly informative normal priors
174 with zero mean for fixed parameters and default vague priors for the intercepts (see appendix S2). We
175 ran four parallel chains and 10,000 iterations (5,000 discarded as burn-in) and ensured convergence with
176 R-hat values being <1.01 for all parameters. Model fit was assessed with posterior-predictive checks
177 using the package *bayesplot* v1.8.0 ([Gabry et al., 2019](#); [Gabry & Mahr, 2019](#); see appendix Fig. S2). We
178 report 90% credible intervals (Crl) for posterior samples, which do not overlap zero when 95% of the
179 posterior is either above or below zero, and we calculated conditional and marginal Bayes R^2 ([Gelman et](#)
180 [al., 2019](#)) to assess how much variation is explained by the treatments or varying intercepts.

181 *Direct and indirect effects of land use on establishment*

182 To evaluate how grazing, mowing and productivity modify or create regeneration spaces and hence
183 determine the number of established seeding species, we modelled the absolute difference in sown
184 species richness between the seeding treatments and control (Δ richness) as well the difference in total
185 species richness. We fitted two separate multivariate models for seeding (only) and seeding and
186 disturbance (combined) treatments in the first and in the fifth year. Multivariate models sample the
187 parameters jointly for the sub-models and, thus, allow modelling response variables measured on the
188 same experimental unit. We expected direct effects of grazing (log-transformed grazing days ha^{-1}),
189 mowing frequency and productivity (log-transformed $g m^{-2}$) on establishment and included region
190 effects as well as an effect of Δ richness of year one on year five (see also Fig. 2). Because fertilization
191 intensity (log-transformed $kg Nitrogen ha^{-1}$) was closely correlated to mowing frequency ($\rho=0.66$, Vogt
192 et al., 2019), we included only an indirect effect of fertilization on Δ richness via productivity. We
193 modelled productivity with Gamma distribution and log link and assumed Gaussian errors for Δ richness.
194 The repeated biomass measurements were simultaneously modelled as arising from a normal
195 distribution with a mean equal to the 'true' latent productivity of each grassland site and measurement
196 error σ . We chose arithmetic means and standard deviations of harvested biomass as informed priors
197 for the means of latent productivity, (i.e., varying between grasslands) and a weakly informative prior
198 for the measurement error σ (see appendix S4). The multivariate models were estimated using *rstan*
199 v2.21.2 (Stan Development Team, 2020).

200 *Plant functional traits effects on establishment*

201 To explore how functional traits affect the establishment of sown species five years after seeding along
202 the productivity gradient, we modelled establishment with logistic regression. We assumed sown
203 species to have successfully established in the seeding treatments if they were present in year five.
204 Because some of the sown species may have been present before the start of the experiment, we only

205 judged whether a species successfully established when the species was absent on either the control or
206 disturbance-only treatment in any year. We kept 2,746 observations, because sown species were
207 already present in the respective grasslands in 37% of the cases in the Alb region, 36% in the Hainich
208 region and 21% in the Schorfheide region (see Tables S3 and S4). This definition is conservative,
209 especially for common species, but reduces the number of false positive observations where a sown
210 species was already present. From the LEDA Traitbase (Kleyer et al., 2008) we extracted specific leaf
211 area (relative growth rate), canopy height (competitive ability of the adult plant) and seed mass (energy
212 for seedling recruitment) and averaged the trait values by species.

213 To test for the effects of traits and trait-environment interactions on establishment, we modelled binary
214 establishment with logit link function as a function of height (log.), seed mass (log.) and specific leaf
215 area. We included seeding density as a categorical predictor. Informed by a negative effect of
216 productivity on the number of established species, we initially included productivity (log-transformed, as
217 a measure of competition) and interactions of traits with productivity. We included varying intercepts
218 for both species identity and grassland site due to the multi-level structure and scaled all predictors to
219 unit standard deviation. Productivity was again modelled as latent (see appendix S5).

220 To test for trait-grazing and trait-mowing effects, we fitted three additional models with i) trait-grazing
221 interactions, ii) trait-mowing interactions and iii) both trait-grazing and trait-mowing interactions in
222 addition to trait-productivity interactions. To judge whether including grazing and mowing interactions
223 improved the prediction of establishment, we compared models based on the expected log point-wise
224 predictive density from leave-one-out cross-validation (Vehtari et al., 2017; Vehtari et al., 2020).

225

226 RESULTS

227 *Seeding and disturbance effects on plant diversity*

228 High-diversity seeding had clear positive effects on species richness over the five years of this study, but
229 less so on S_{PIE} , which accounts for community evenness. The seeding effect on species richness increased
230 steadily over time, from slightly positive in the first year to clearly positive in the fifth year (seeding β
231 =0.04, 90% Crl: -0.0 to 0.1, plus seeding*5th year β =0.09, 90% Crl: 0.0 to 0.2; Fig. 1a; appendix Table S1).
232 Transformed to the response scale with average species richness of 25.7 per 4 m² on the control, this
233 resulted in an increase in 3.1 species in year five (Fig. 1c). Seeding alone had no clear effect on S_{PIE} (Fig.
234 1a, f), which suggests that increases in richness were compensated by decreases in evenness because
235 the sown species established with low abundance. Disturbance led to temporary increases in both
236 species richness and S_{PIE} (Fig. 1a, b, e), indicating the germination of ruderal species and an increase in
237 evenness after disturbance.

238 Both species richness and S_{PIE} considerably increased when seeding and disturbance were combined. For
239 species richness, the seeding and disturbance interaction was clearly positive in the first year but
240 became weaker over time (seeding*disturbance β =0.25, 90% Crl: 0.2 to 0.3, plus
241 seeding*disturbance*5th year β =-0.16, 90% Crl: -0.3 to -0.1; Fig. 1a, d; appendix Table S1). S_{PIE} was also
242 positively affected by the seeding*disturbance interaction (seeding*disturbance β =0.15, 90% Crl: 0.0 to
243 0.3), but temporary increases in S_{PIE} were mainly driven by the disturbance effect (e.g. disturbance*2nd
244 year β =0.15, 90% Crl: 0.0 to 0.3; Fig. 1a, e). On the response scale, the combination of seeding and
245 disturbance led to an increase in species richness by 8.3 species in the fifth year (Fig. 1d) and an increase
246 in S_{PIE} by 0.6 (Fig. 1g), given an average S_{PIE} of 6.2 on the control.

247 *Direct and indirect effects of land use on establishment*

248 We found no direct effects of grazing or mowing on the number of established species (Δ richness), but
249 fertilization indirectly limited the long-term establishment on the combined treatment via a negative
250 effect of productivity on Δ richness in year five (Fig. 2b, d; appendix Tables S2 and S3). Δ richness in
251 the first year was less related to productivity or land use, underlined by lower R^2 values for both
252 treatments compared to the fifth year (Fig. 2). Instead, Δ richness of the combined treatment in the first
253 year was higher when considering all species (Intercept $\alpha=9.84$, 90% CrI: 8.4 to 11.2; Fig. 2b) compared
254 to Δ richness of seeding species (Intercept $\alpha=6.10$, 90% CrI: 5.2 to 7.0; Fig. 2d), which suggests a
255 considerable but temporary contribution of ruderal species to Δ richness after disturbance. However,
256 sown species Δ richness increased until the fifth year, and the difference to Δ richness considering all
257 species decreased considerably (Fig. 2b, d). The negative effect of productivity on Δ richness was less
258 clear for the seeding-only treatment, but turned from neutral to weakly negative over time for sown
259 species Δ richness (Fig. 2a, c).

260 *Plant functional traits effects on establishment*

261 Plant functional traits considerably influenced establishment, but effects of traits on establishment
262 interacted with productivity. Establishment was consistently predicted by productivity, specific leaf area
263 and their interaction (Fig. 4c, d). Productivity decreased establishment drastically such that the
264 probability of successful establishment in year five was almost zero in productive grasslands for the
265 seeding-only and seeding and disturbance treatments (insets in Fig. 4). Species with low specific leaf
266 area had higher average establishment success, but trait-productivity interactions for both seeding
267 treatments indicate that species with low specific leaf area established increasingly better at low-
268 productivity sites (Fig. 4c, f). The effects of height and seed mass remained largely unclear (Fig. 4a, b, d,
269 e), but the trait-productivity interactions suggest that species with high seed mass established better at
270 highly productive sites in the combined treatment (Fig. 4e). We tested for additional trait-grazing and

271 trait-mowing interaction effects on establishment, but based on leave-one out cross-validation, neither
272 interaction improved the prediction of establishment success (appendix Table S7).

273 A high seeding density, which was related to small seeds (cf. Methods) increased establishment rates for
274 both seeding-only ($\beta=1.83$, 90% CrI: 0.8 to 3.0, appendix Table S4) and seeding and disturbance
275 treatments ($\beta=2.03$, 90% CrI: 1.2 to 2.9). The effects on establishment on the seeding-only treatment
276 were less clear, as overall parameter uncertainty was higher and average establishment success lower
277 (Intercept $\alpha=-4.06$, 90% CrI: -4.7 to -3.5) compared to the combined treatment (Intercept $\alpha=-2.54$, 90%
278 CrI: -3.0 to -2.1). The marginal Bayes R^2 was considerably lower than the conditional R^2 for both seeding
279 treatments (seeding only: median $R_{marg}^2=0.23$, $R_{cond}^2=0.45$; seeding and disturbance: median R_{marg}^2
280 $=0.27$, $R_{cond}^2=0.42$), which implies that grassland site and species identity accounted for a considerable
281 share of variance not explained by traits.

282

283 **DISCUSSION**

284 The ongoing biodiversity crisis reflects an urgent need to restore plant diversity in grasslands wherever
285 possible, but predicting restoration success is remarkably difficult (Brudvig et al., 2017), and restoration
286 actions need to be carefully adapted to local site conditions (Laughlin, 2014; Török & Helm, 2017). Our
287 results highlight the potential for using high-diversity seed mixtures to restore plant diversity across a
288 wide range of permanent grasslands, especially when combined with soil disturbance. However,
289 productivity limited the overall establishment success of sown species and shaped establishment via an
290 interaction with plant functional traits. We demonstrate that productivity is a major constraint for the
291 restoration of plant diversity in managed grasslands, but productivity can be used as an indicator to plan
292 restoration actions and select suitable target species along productivity gradients.

293 The most effective method for increasing plant diversity was the combination of seeding and topsoil
294 disturbance. This finding is well in line with early results from this experiment (Klaus et al., 2017) and
295 confirms previous studies, which conclude that species richness is largely limited by dispersal limitation
296 and the lack of a persistent soil seed bank for most species (Clark et al., 2007; Klaus et al., 2018; Myers &
297 Harms, 2009). Concurrent with previous research, disturbing the topsoil reduced microsite limitations
298 and effectively created regeneration space for the seeded species to establish (Bischoff et al., 2018;
299 Grubb, 1977; Münzbergová & Herben, 2005). Yet, over the five years of this study, species richness
300 slowly increased in the seeding-only treatment as well. This suggests that at least some species can
301 establish without topsoil disturbance, for instance when microsites are created by grazing (Kladivová &
302 Münzbergová, 2016; Maccherini & Santi, 2012).

303 While we observed clear seeding effects on species richness, we found weaker effects on the effective
304 number of species S_{PIE} , indicating that increases in richness were partly outweighed by decreases in
305 community evenness due to low cover of the newly established species. In contrast to Ladouceur et al.
306 (2020), who reported positive effects of seeding-only on S_{PIE} across a range of natural and semi-natural
307 grasslands, in our study the lack of a seeding-only effect on S_{PIE} suggests that when the disturbance was
308 not applied, sown species had not yet become important members of the community. A possible
309 explanation is that a higher average productivity of our grasslands limits establishment more strongly
310 compared to the partially degraded grasslands included in the study by Ladouceur et al. (2020). The
311 weaker positive effects of the seeding treatments on S_{PIE} due to increases in evenness suggest that
312 creating microsites is important for the introduced species to establish with noticeable cover, but it
313 remains an open question as to how long these differences persist.

314 We found no direct effects of land-use intensity on the number of established seeding species, but
315 fertilization indirectly limited long-term establishment via a negative effect of productivity. At first, the

316 intensively used productive grasslands benefited most from seeding and disturbance (Klaus et al., 2017),
317 but initial increases in species richness were recorded right after the set-up of the experiment, before
318 the first mowing or grazing management, and were partly driven by ruderal species from the soil seed
319 bank. While previous studies reported that productivity limits seeding successes in grasslands (Dickson &
320 Foster, 2008; Foster, 2001), our study is the first to confirm this pattern along a realistic grassland
321 productivity gradient. The increasing impact of productivity on establishment over time suggests that
322 enhancing plant diversity through seeding is only an ephemeral success in productive grasslands and
323 highlights that recruitment limitation is at least as important a constraint for species richness as
324 dispersal limitation (Clark et al., 2007; Münzbergová & Herben, 2005). Concurrently, the number of
325 established species correlated positively with the resident species richness (see appendix S6), both of
326 which are constrained by productivity (Socher et al., 2012). Thus, productivity limits both resident
327 species richness and the establishment of introduced species, indicating that both species richness and
328 the potential to introduce new species decrease with higher fertilization, which increases productivity.

329 Several studies have emphasized that soil fertility and its determinant role for productivity as one of the
330 most important constraints to restoring species-rich grasslands (Dickson & Foster, 2008; Walker et al.,
331 2004), and fertilization significantly contributes to this constraint. However, we were not able to identify
332 a threshold of productivity at which restoration would change from successful to failed. Our results
333 suggest that the establishment success is generally low at productivity levels above ~250 g m⁻²
334 aboveground green biomass in May, but the establishment probably still depends to a significant extent
335 on further site characteristics. One such factor that determines seedling establishment might be litter
336 biomass. While small amounts of litter can facilitate seedling recruitment in dry grasslands, dense litter
337 (>500 g m⁻²) largely inhibits recruitment (Loydi et al., 2013). However, we rarely observed significant
338 amounts of litter in our grasslands, which is typical for regularly used Central European grasslands (Gross
339 et al., 2009).

340 Interestingly, grazing and mowing had no effect on the number of established species. Grazing is
341 assumed to create microsites by feeding and trampling and, hence, can increase the recruitment from
342 seeds (Kladivová & Münzbergová, 2016), but effects of grazing on establishment are usually low
343 (Maccherini & Santi, 2012; Rasran et al., 2007). In our study, bare soil cover was hardly related to grazing
344 or mowing intensities (appendix Fig. S9). We suspect that productivity partly reflects the availability of
345 microsites, because sparse vegetation with low aboveground biomass provides more space per se, or
346 because the effects of grazing and mowing on microsites were overruled by productivity. Based on our
347 results, we conclude that, in fertile grasslands, productivity must be reduced to ensure restoration
348 success. The main focus in productive grasslands, therefore, must be to stop fertilization and reduce the
349 soil nutrient loads, before fine-tuning the grazing and mowing management.

350 Plant functional traits clearly affected establishment. Sown species with a low specific leaf area
351 consistently established better, independent of productivity. However, the patterns we observed for the
352 seeding-only treatment were less clear, probably due to generally lower establishment rates and
353 subsequently greater uncertainty in the relationships between traits and establishment. When seeding
354 was combined with disturbance, we also found that less competitive species with low canopy height and
355 low seed mass (such as *Dianthus carthusianorum* or *Sanguisorba minor*) tended to establish better. In
356 part, these main effects were likely driven by the fact that the overall establishment rate decreased with
357 productivity. At low levels of productivity, the plant community is characterized by species with a low
358 specific leaf area (Allan et al., 2015), as conservative and slow-growing species with low specific leaf area
359 have no disadvantage in establishing and are possibly better adapted to less fertile environments.

360 Such adaptations to the environment are reflected in the interactions between functional traits and
361 productivity that shape establishment during restoration. For instance, in the combined treatment,
362 species with high seed mass established better in productive sites. Having considerable energy stored in

363 large seeds increases recruitment rates (Clark et al., 2007) and seedling survival rates (Metz et al., 2010),
364 which seems to be a particular advantage in productive sites, where competition with the regrowing
365 vegetation selects for the most competitive seedlings. In contrast, species with low specific leaf area
366 established better at sites of low productivity. The fast resource-acquisition strategy of species with high
367 specific leaf area is beneficial under nutrient-rich conditions, for instance resulting from intensive
368 fertilization (Allan et al., 2015; Vries et al., 2012). Our results confirm the finding that this adaption to
369 nutrient surplus in productive sites does not represent an advantage under conditions with less
370 competition for light (Zirbel & Brudvig, 2020), where, for instance, water availability limits plant growth.
371 We propose that sown species in grasslands are environmentally filtered by productivity and successful
372 establishers possibly reflect the traits of the resident plant community (Ames et al., 2020; Breitschwerdt
373 et al., 2015). Variation in establishment success along environmental gradients and trait-environment
374 interactions are rarely studied, but insights on these relationships provide valuable information to
375 prioritize restoration sites and compile site-specific seed mixtures to maximise success and ecosystem
376 functions during restoration (Balazs et al., 2020; Laughlin, 2014)

377

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391

392 **AUTHORS' CONTRIBUTIONS**

393 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
394 M.F. collected the data, M.F. analysed the data and led the writing of the manuscript. All authors
395 contributed critically to the drafts and gave final approval for publication.

396

397 **DATA AVAILABILITY STATEMENT**

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

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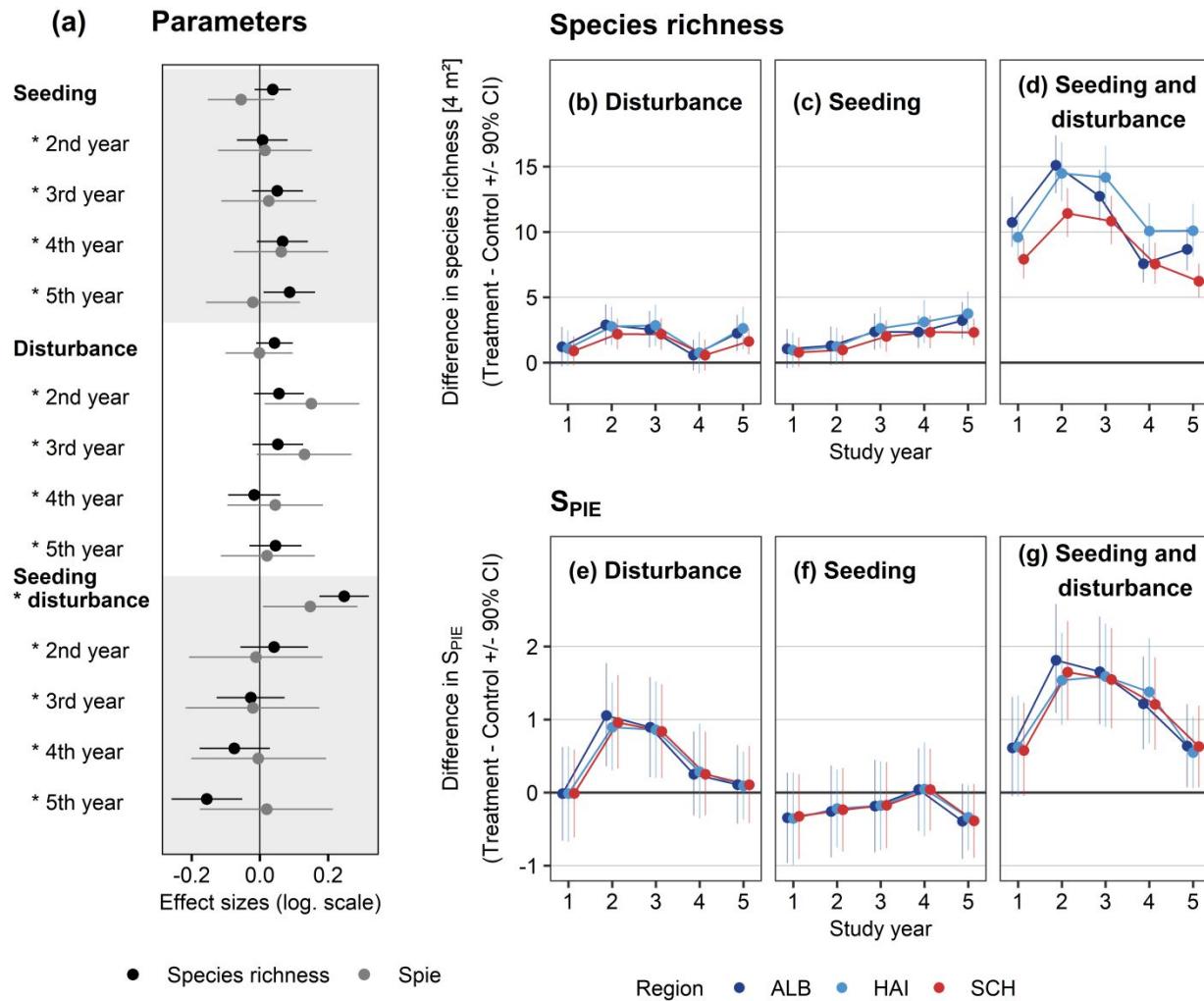
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588 **FIGURES AND TABLES**

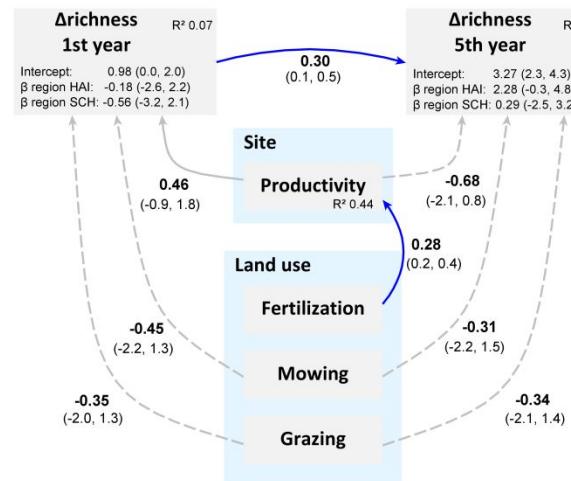
589

590 Figure 1: Effects of seeding and soil disturbance on species richness and S_{PIE} over time. (a) Effect sizes of
 591 seeding, disturbance and the seeding and disturbance interaction, as the main and interacting effects
 592 with years, for species richness and S_{PIE} (intercept, year main effects and varying intercepts not shown,
 593 see appendix Table S1). Both diversity measures were modelled with log-link assuming Poisson and
 594 Gamma error structure, respectively. Panels (b) to (g) display differences between treatments and the
 595 control on the response scale. Seeding alone had small positive effects on species richness, which
 596 increased over time (c), while this was not found for S_{PIE} (f). The combination of seeding and disturbance
 597 had a clear positive effect on both diversity metrics, although it was weaker for S_{PIE} . To calculate

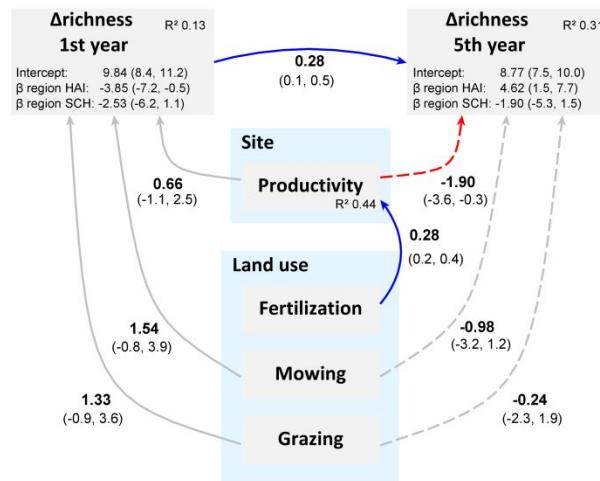
598 differences between treatments and control, we predicted species richness and S_{PIE} based on additive
599 parameter effects (a), transformed predicted values to the response scale and calculated the difference
600 in predicted values between treatments and control. Points indicate medians along with 90% CrI.

Species richness

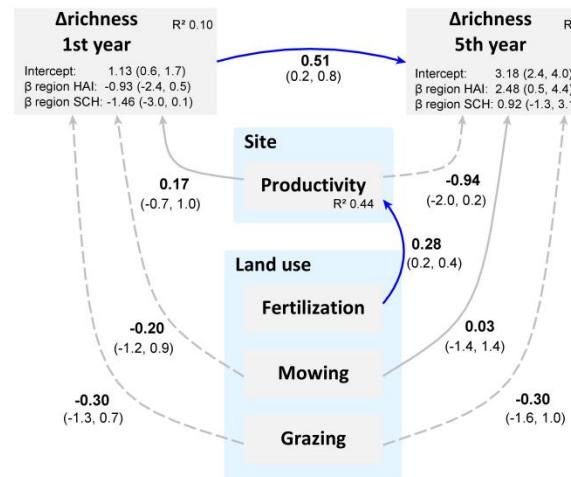
(a) Seeding only



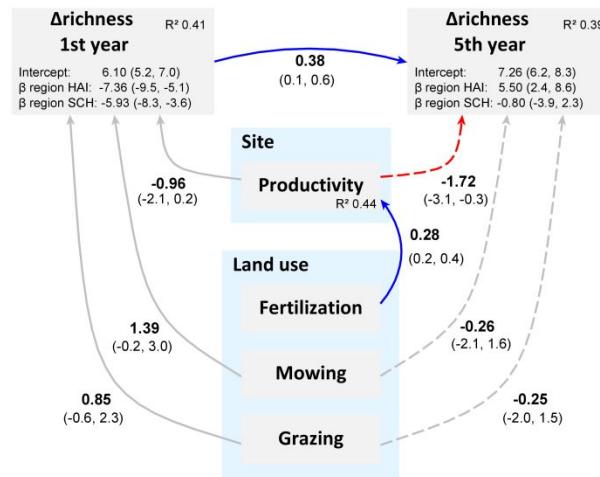
(b) Seeding and disturbance

**Species richness of sown species**

(c) Seeding only



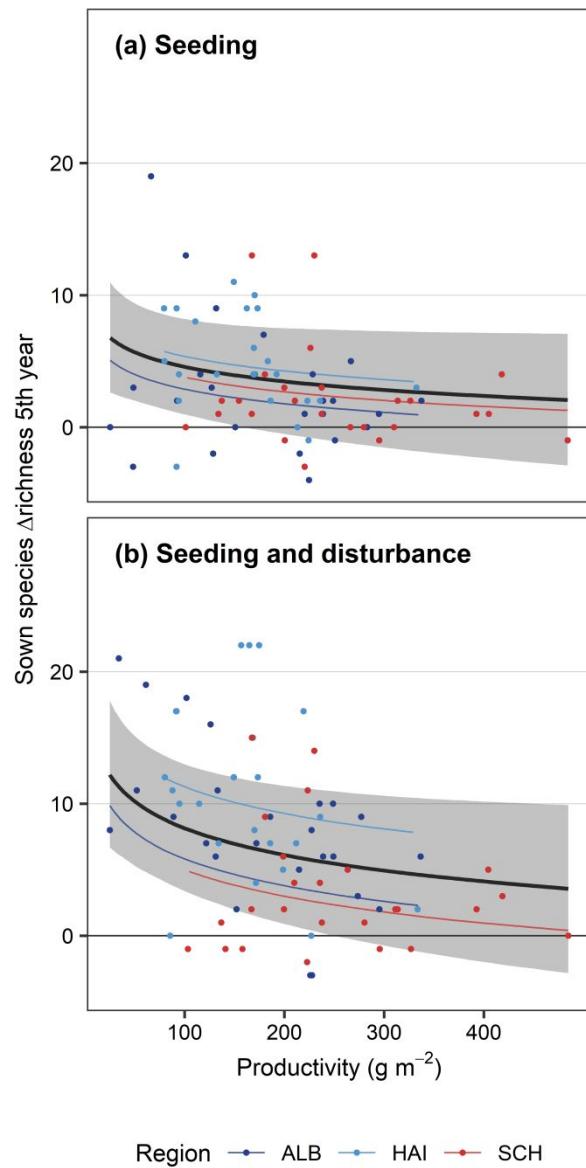
(d) Seeding and disturbance



601

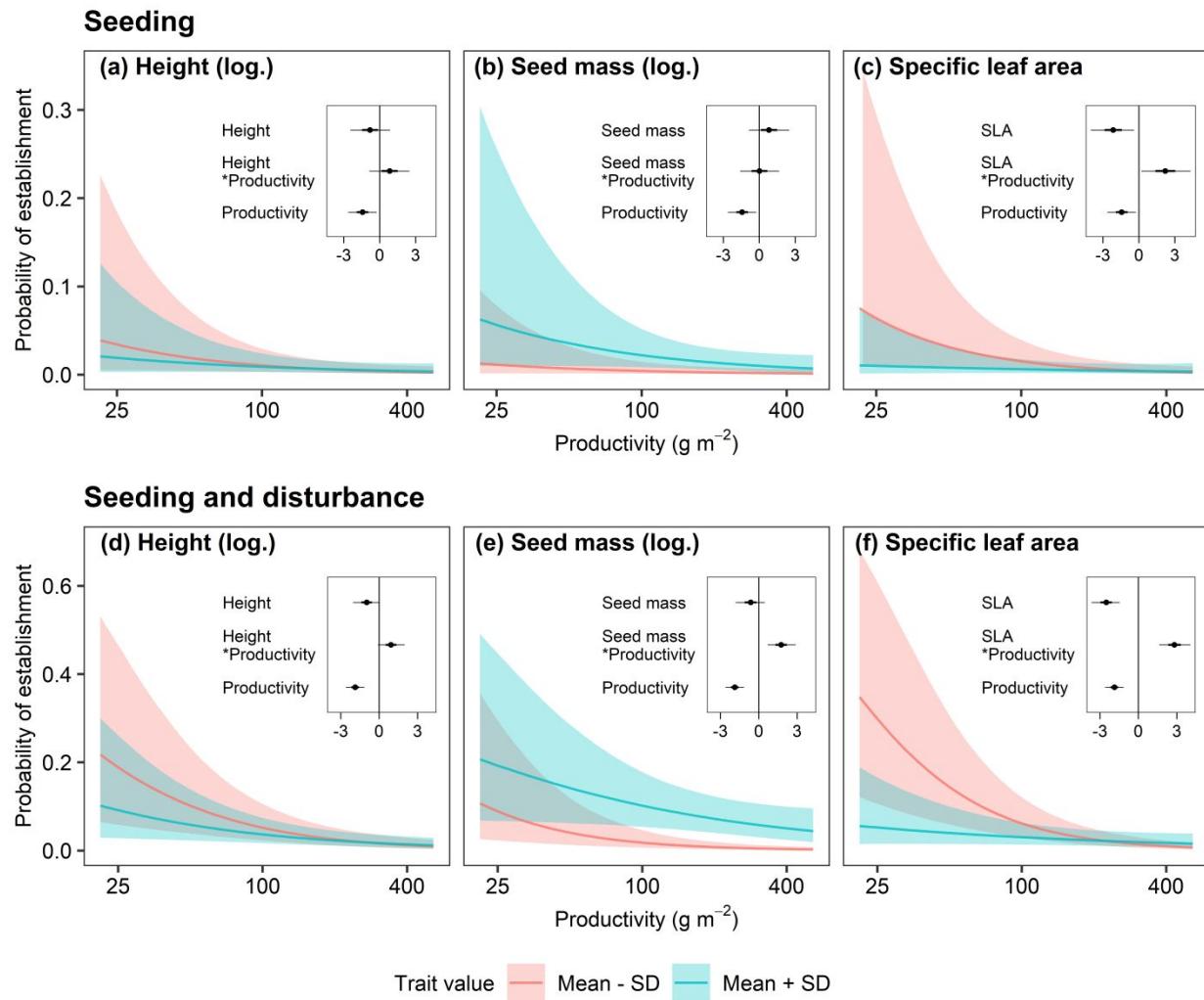
602 Figure 2: Direct and indirect land-use effects on the number of established species (Δ richness, the
 603 difference in species richness between treatment and control) for total species richness and sown
 604 species richness. Land-use effects on Δ richness were absent on the seeding-only treatment (a, c).
 605 Fertilization had an indirect negative effect via productivity on Δ richness in the fifth year for both (b)
 606 total and (d) sown species richness on the seeding and disturbance treatment. In the first year after
 607 disturbance, the larger Δ richness for total species richness indicates a considerable increase in unsown
 608 species on the seeding and disturbance treatment, which almost completely vanished in the fifth year.

609 Positive paths are shown as solid and negative paths as dashed lines along with standardized regression
610 coefficients and 90% CrI, in blue (positive) and red (negative) when the CrI does not overlap zero. Fixed
611 effects of region are displayed in the Δ richness boxes.



612

613 Figure 3: Conditional effect of productivity on the number of established sown species as compared to
 614 the control (Δ richness) in the fifth year. (a) Overall sown species Δ richness was lower and the effect of
 615 productivity weak on the seeding-only treatment, (b) but sown species Δ richness declined with
 616 productivity on the combined treatment. Lines denote the median and 90% CrI of sown species Δ
 617 richness across all 73 grasslands (grey) and within regions (coloured), conditioned on mean values of the
 618 other predictors (see Fig. 2 c, d).



619

620 Figure 4: Conditional effects of plant height, seed mass, specific leaf area and productivity (log scale) on
 621 the establishment of sown species on (a)-(c) the seeding-only and (d)-(f) the seeding and disturbance
 622 treatments. Especially in the combined treatment, trait effects on establishment interacted considerably
 623 with productivity. Coloured lines denote the median and 90% CrI for low (mean minus one SD, red) and
 624 high (mean plus one SD, blue) trait values, conditioned on mean values of the other traits and mean
 625 sowing density. In each panel, inset plots show the median and 90% CrI of the parameters used for
 626 prediction. See Table S4 for details.

Supporting information to: Restoration of agricultural grasslands by seeding: assessing the limiting factors along land-use gradients

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S1 Experimental design

We established a 2*2 factorial experiment with seeding and soil disturbance in 73 grasslands. The four experimental treatments (control, seeding only, seeding and disturbance, disturbance only) each had a size of 7 m*7 m and were arranged in a rectangle (or sometimes in a row, if the grassland shape or site characteristics did not allow for a rectangle) with 2 m distance between treatments. Within each of the treatments, we surveyed vegetation in one 2 m * 2 m quadrat and sampled biomass each year in four 0.25 m² squares (Fig. S1). We sampled biomass in different squares on the control each year because sampled soil cores after biomass sampling in some years, which would have affected biomass samples in the following years. See (Klaus et al., 2017) for further details on the experimental design.

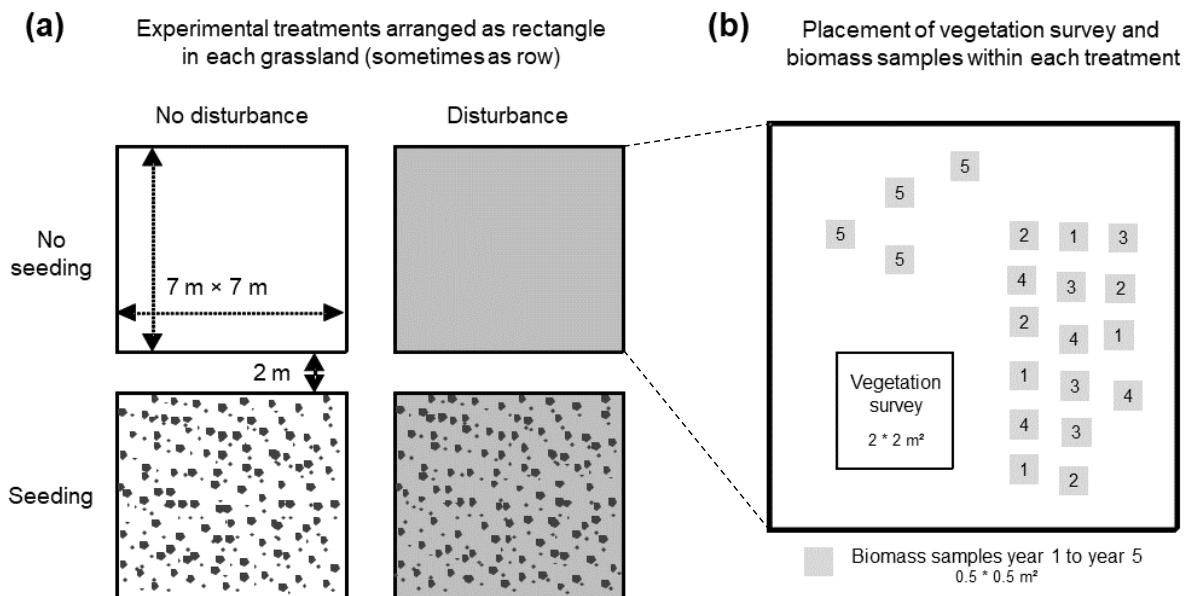


Figure S1: Design of the seeding and disturbance experiment on the 73 grasslands under study. (a) The four treatments (control, seeding, seeding and disturbance, disturbance) were arranged in a rectangle. (b) Within each treatment, we surveyed vegetation on 2 m * 2 m and sampled biomass on four 0.5 m * 0.5 m squares. We sampled biomass in different squares each year.

S2 Seeding and disturbance effects on plant diversity

S2.1 Model formulas

S2.1.1 Plant species richness

$Species\ richness_i \sim \text{Poisson}(\mu_i)$, with

$$\begin{aligned} \log(\mu_i) = & \alpha + \beta_1 * Disturbance_{i[j][k]} + \beta_2 * Seeding_{i[j][k]} \\ & + \beta_3 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} + \\ & + \beta_4 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year2_{i[j][k]} \\ & + \beta_5 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year3_{i[j][k]} \\ & + \beta_6 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year4_{i[j][k]} \\ & + \beta_7 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year5_{i[j][k]} \\ & + Grassland_{i[j]} + RegionYear_{i[k]} \end{aligned} \quad (1)$$

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

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

S2.1.2 S_{PIE}

$S_{PIE,i} \sim \text{Gamma}(\mu_i, \phi)$

$$\begin{aligned} \log(\mu_i) = & \alpha + \beta_1 * Disturbance_{i[j][k]} + \beta_2 * Seeding_{i[j][k]} \\ & + \beta_3 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} + \\ & + \beta_4 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year2_{i[j][k]} \\ & + \beta_5 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year3_{i[j][k]} \\ & + \beta_6 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year4_{i[j][k]} \\ & + \beta_7 * Disturbance_{i[j][k]} * Seeding_{i[j][k]} * year5_{i[j][k]} \\ & + Grassland_{i[j]} + RegionYear_{i[k]} \end{aligned} \quad (2)$$

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

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

S2.1.3 Priors for the species richness and S_{PIE} models:

$$\begin{aligned} \alpha &\sim \text{StudentT}(\nu = 3, \mu = 3, \sigma = 10) \\ \beta &\sim \text{Normal}(\mu = 0, \sigma = 2) \\ \frac{1}{\phi} &\sim \text{Gamma}(\alpha = 0.01, \beta = 0.01) \end{aligned} \quad (3)$$

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

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

Because both species richness and S_{PIE} were modelled with log-link, we specified identical priors for β .

$Disturbance_{i[j][k]}$, $seeding_{i[j][k]}$ and $year_{i[j][k]}$ are dummy variables for treatments and year for $Grassland_j$ and $RegionYear_k$. $Grassland_j$ is the grassland site grouping factor (73 grasslands) and $RegionYear_k$ is the region times year interaction grouping factor (three regions and five years).

S2.2 Model diagnostics

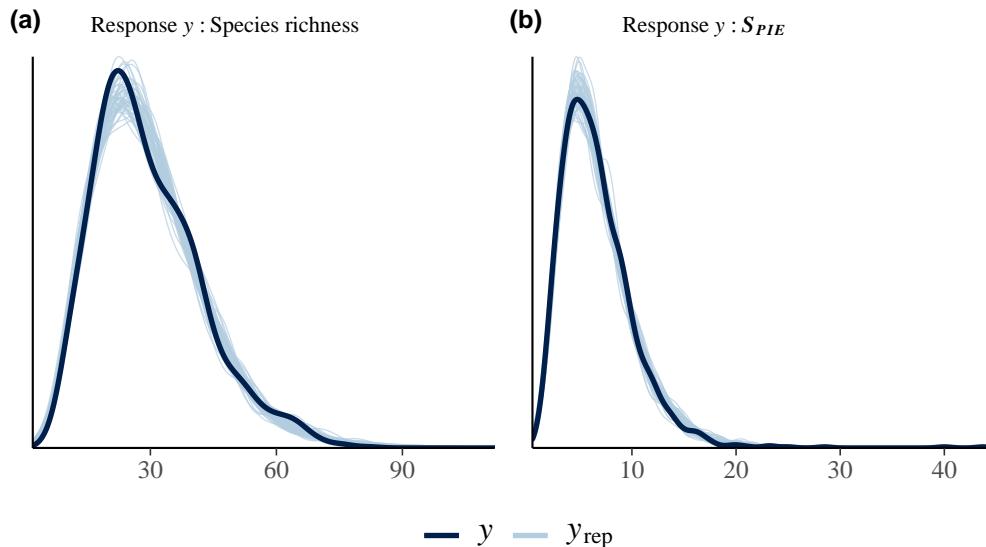


Figure S2: Kernel density estimates of observations (y) for (a) species richness and (b) S_{PIE} , and 50 draws from the (y_{rep}) posterior predictive distribution.

S2.3 Parameter credible intervals

Table S1: Effects of seeding, disturbance, year and their interactions on plant species richness and S_{PIE} diversity in the 73 grasslands. Given here are the mean and the 90% credible interval and effective sample size of the posterior samples. 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, the year five effect and the seeding times year five interaction. Credible intervals which do not overlap zero are shown in bold. Note that species richness was modelled assuming Poisson errors with log-link, while S_{PIE} was modelled as Gamma distributed with log-link. R-hat values <1.01 for all parameters indicated chain convergence.

	Species richness				S_{PIE}			
	5 %	50 %	95 %	N_{eff}	5 %	50 %	95 %	N_{eff}
Intercept	2.96	3.18	3.39	2559	1.72	1.85	1.99	3448
Disturbance	-0.01	0.04	0.10	3259	-0.10	0.00	0.10	4774
Seeding	-0.02	0.04	0.09	3098	-0.15	-0.05	0.04	4508
Year 2	-0.25	0.04	0.33	3243	-0.22	-0.06	0.09	6255
Year 3	-0.24	0.04	0.33	3327	-0.18	-0.02	0.14	6228
Year 4	-0.32	-0.02	0.27	2793	-0.23	-0.07	0.09	5992
Year 5	-0.34	-0.05	0.26	3003	-0.38	-0.22	-0.06	6185
Disturbance*Seeding	0.17	0.25	0.32	2707	0.01	0.15	0.29	4397
Disturbance*Year 2	-0.02	0.06	0.13	4169	0.01	0.15	0.29	6077
Disturbance*Year 3	-0.02	0.05	0.13	4081	-0.01	0.13	0.27	6204
Disturbance*Year 4	-0.09	-0.02	0.06	4188	-0.10	0.05	0.18	6146
Disturbance*Year 5	-0.03	0.05	0.12	4068	-0.11	0.02	0.16	6242
Seeding*Year 2	-0.07	0.01	0.08	4086	-0.12	0.01	0.15	5860
Seeding*Year 3	-0.02	0.05	0.13	3956	-0.11	0.03	0.17	5985
Seeding*Year 4	-0.01	0.07	0.14	4177	-0.08	0.06	0.20	5863
Seeding*Year 5	0.01	0.09	0.16	3966	-0.16	-0.02	0.12	6017
Disturbance*Seeding*Year 2	-0.06	0.04	0.14	3535	-0.21	-0.01	0.18	5602
Disturbance*Seeding*Year 3	-0.13	-0.03	0.07	3396	-0.22	-0.02	0.17	5650
Disturbance*Seeding*Year 4	-0.18	-0.07	0.03	3623	-0.20	0.00	0.19	5627
Disturbance*Seeding*Year 5	-0.26	-0.16	-0.05	3283	-0.18	0.02	0.21	5831
SD Grassland	0.28	0.32	0.38	1514	0.29	0.34	0.39	2967
SD RegionYear	0.11	0.20	0.35	1276	0.05	0.09	0.15	4303
ϕ					7.40	7.88	8.37	14113
R^2_{cond}	0.85	0.86	0.87		0.40	0.43	0.46	
R^2_{marg}	0.11	0.15	0.25		0.04	0.06	0.09	

S3 Treatment effects over time on litter cover and bare soil

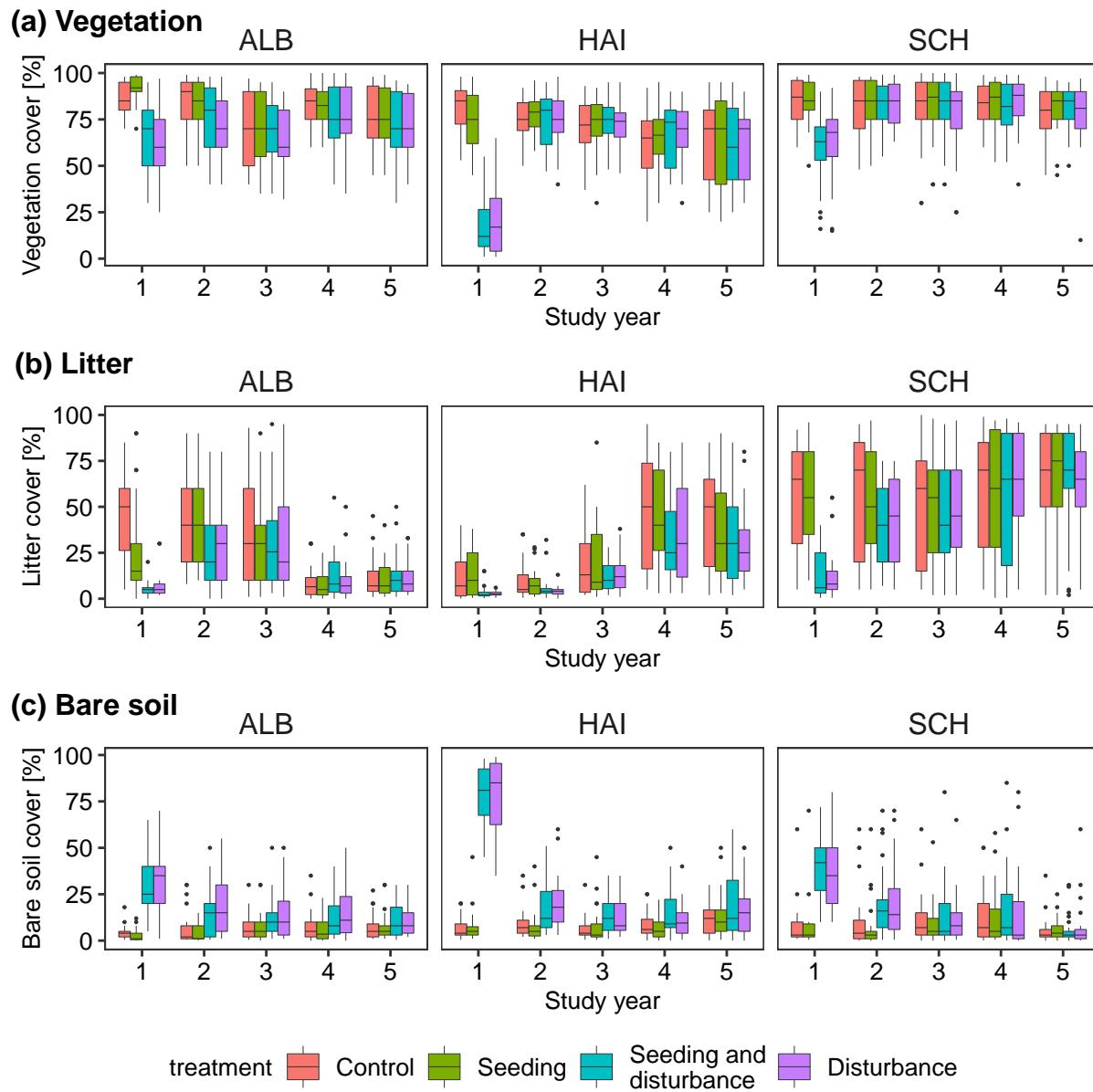


Figure S3: Cover of (a) vegetation, (b) litter and (c) bare soil on the experimental treatments in the three regions as estimated during field sampling, as estimated visually. Topsoil disturbance decreased vegetation and litter cover and increased bare soil cover in the first year, but this effect vanished quickly. Note that there are considerable observer effects on cover estimates. For instance, the main observers in the ALB and HAI region changed after year 3, which led to large changes in estimated vegetation and litter covers.

S4 Direct and indirect effects of land use on enrichment

S4.1 Model formulas

S4.1.1 Δ richness of sown species between seeding treatments and control

$$\begin{aligned} \Delta \text{richness } 1st \text{ year}_i &\sim \text{Normal}(\mu_i, \sigma_{1st \text{ year}}) \\ \mu_i &= \alpha + \beta_1 * \log(Grazing_i + 1) + \beta_2 * Mowing_i \\ &\quad + \beta_3 * \log(Productivity_i) \\ &\quad + \beta_4 * RegionHAI_i + \beta_5 * RegionSCH_i \end{aligned} \tag{4}$$

$$\begin{aligned} \Delta \text{richness } 5th \text{ year}_i &\sim \text{Normal}(\mu_i, \sigma_{5th \text{ year}}) \\ \mu_i &= \alpha + \beta_1 * \log(Grazing_i + 1) + \beta_2 * Mowing_i \\ &\quad + \beta_3 * \log(Productivity_i) \\ &\quad + \beta_4 * RegionHAI_i + \beta_5 * RegionSCH_i \\ &\quad + \beta_6 * \Delta \text{richness } 1st \text{ year}_i \end{aligned} \tag{5}$$

$$\begin{aligned} Productivity_i &\sim \text{Gamma}(\mu_i, \phi) \\ \log(\mu_i) &= \alpha + \beta_1 * \log(Fertilization_i + 1) \\ &\quad + \beta_2 * RegionHAI_i + \beta_3 * RegionSCH_i \end{aligned} \tag{6}$$

$$Biomass_{j[i]} \sim \text{Normal}(Productivity_i, \sigma_{error}) \tag{7}$$

Priors for Δ richness in first and fifth year models (6, 7):

$$\begin{aligned} \alpha &\sim \text{StudentT}(\nu = 3, \mu = 3, \sigma = 10) \\ \beta &\sim \text{Normal}(\mu = 0, \sigma = 10) \\ \sigma &\sim \text{Cauchy}(\mu = 0, \sigma = 10), \text{ constrained to be positive} \end{aligned} \tag{8}$$

Priors for productivity model (8):

$$\begin{aligned} \alpha &\sim \text{StudentT}(\nu = 3, \mu = 3, \sigma = 10) \\ \beta &\sim \text{Normal}(\mu = 0, \sigma = 10) \\ \sigma &\sim \text{Cauchy}(\mu = 0, \sigma = 10), \text{ constrained to be positive} \end{aligned} \tag{9}$$

Priors for productivity measurement error model (9):

$$\begin{aligned} Productivity_i &\sim \text{Normal}(\mu = GrasslandMean_i, \sigma = GrasslandSD_i) \\ \sigma &\sim \text{Cauchy}(\mu = 0, \sigma = 150), \text{ constrained to be positive,} \end{aligned} \tag{10}$$

$\Delta \text{richness } 1st \text{ year}_i$ and $\Delta \text{richness } 5th \text{ year}_i$ are the absolute differences in sown species richness (i.e. not considering unsown species when calculating richness) the respective seeding treatment and the control, $Grazing_i$ is the mean grazing intensity (in livestock unit * grazing days ha^{-1}), $Mowing_i$ the mean number of cuts per year and $Fertilization_i$ is the mean amount of fertilizer applied ($\text{kg Nitrogen ha}^{-1}$). $Region_{HAI}$ and $Region_{SCH}$ are dummy variables for the region, with $Region_{ALB}$ as the reference level.

$Biomass_{j[i]}$ is the harvested biomass (g m^{-2}) of year j in grassland site i 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. All predictors were scaled to zero mean and unit SD to make effect sizes comparable.

We fitted models with Δ richness of total species richness (i.e., species richness including species which were not sown, such as ruderal species) using identical model specifications.

S4.2 Predictor variable distributions

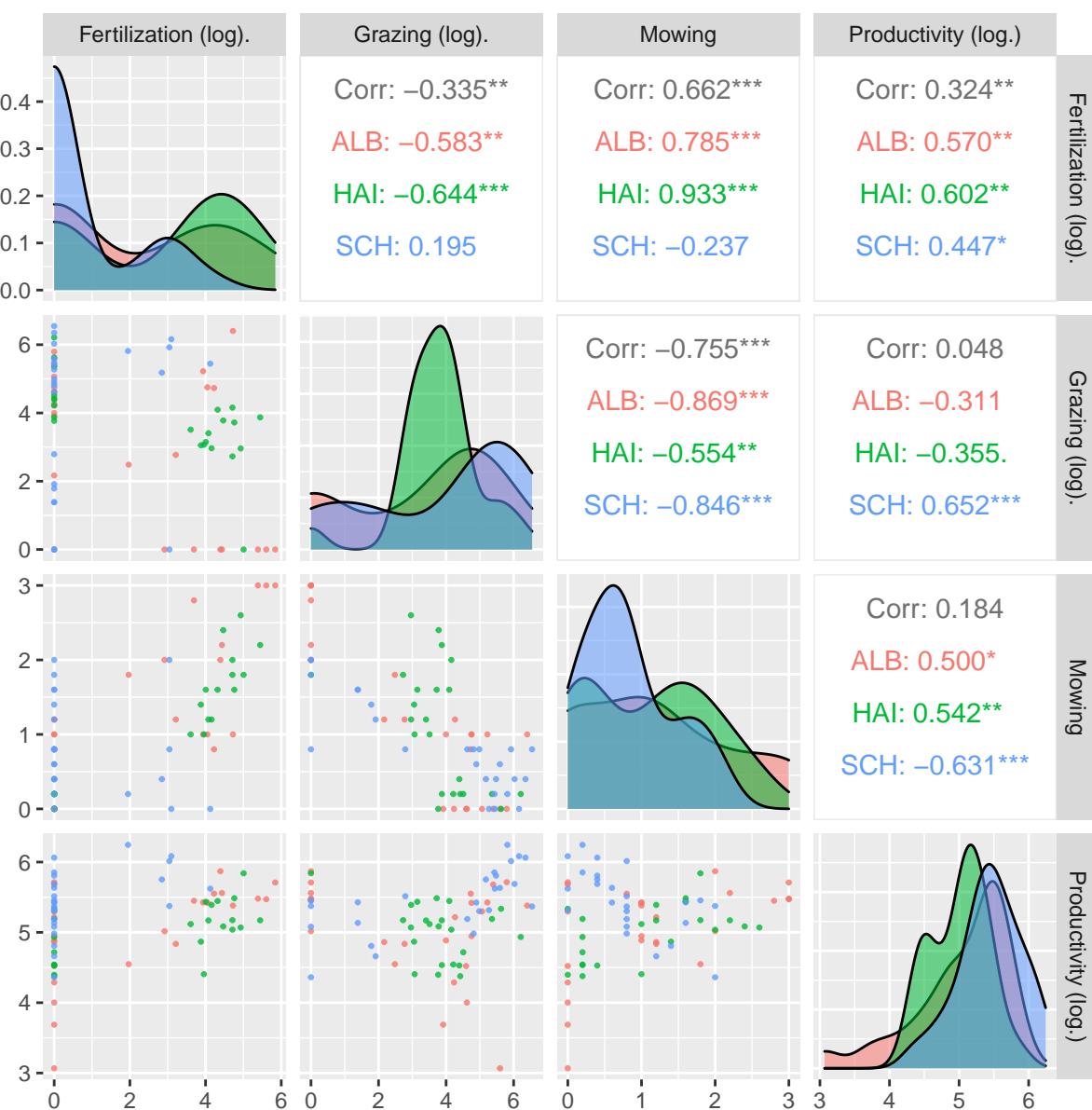


Figure S4: Distribution (diagonal), pairwise scatterplots (lower panels) and correlations of predictor variables among regions (upper panels) as used in the models on direct and indirect effects of land use on the number of established species (Δ richness). Fertilization intensity (in kg N ha^{-1}) and grazing intensity (in livestock unit grazing days ha^{-1}) were $\log(x + 1)$ transformed. Productivity (in aboveground biomass g m^{-2}) was log-transformed and mowing intensity is the mean number of cuts per year. Three grasslands in the ALB region had very low productivity, but parameter estimates were robust to the exclusion of the three grasslands

S4.3 Parameter credible intervals

Table S2: Direct and indirect land-use and region effects on sown species Δ richness, i.e. the difference in sown species richness between the respective treatment and the control. Given here are the mean and the 90% credible interval and effective sample size of the posterior samples. Explained variation of Δ richness 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 Δ richness through productivity. Intercepts of the Δ richness models refer to estimated means in the Alb region given average predictor values, and the intercept of the productivity model refers to zero fertilization in the Alb region. 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 . R-hat values <1.01 for all parameters indicated chain convergence.

	Seeding only				Seeding and disturbance			
	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}
Δ richness 1st year								
Intercept	0.57	1.13	1.70	43873	5.22	6.10	6.97	47515
Region HAI	-2.37	-0.93	0.49	33737	-9.50	-7.36	-5.21	35272
Region SCH	-3.04	-1.46	0.14	19190	-8.29	-5.93	-3.55	25800
Mowing intensity	-1.23	-0.20	0.85	16595	-0.17	1.39	2.96	21279
Grazing intensity (log.)	-1.27	-0.30	0.68	19813	-0.59	0.85	2.31	23729
Productivity (log.)	-0.73	0.17	0.97	11573	-2.12	-0.96	0.22	21615
σ	2.58	2.96	3.44	30403	3.92	4.49	5.22	32177
Δ richness 5th year								
Intercept	2.40	3.18	3.95	44594	6.24	7.26	8.31	46647
Region HAI	0.52	2.48	4.40	32742	2.37	5.50	8.64	24241
Region SCH	-1.26	0.92	3.08	21615	-3.91	-0.80	2.34	25356
Mowing intensity	-1.37	0.03	1.43	19069	-2.11	-0.26	1.60	20820
Grazing intensity (log.)	-1.61	-0.30	1.01	22910	-1.98	-0.25	1.46	22947
Δ richness 1st year	0.23	0.51	0.79	30287	0.14	0.38	0.63	24327
Productivity (log.)	-2.03	-0.94	0.19	15264	-3.11	-1.72	-0.33	21884
σ	3.47	4.00	4.66	28408	4.66	5.36	6.24	34282
Productivity								
Intercept	4.67	4.86	5.04	16607	4.67	4.86	5.04	21596
Region HAI	-0.28	-0.09	0.10	24386	-0.28	-0.09	0.11	26177
Region SCH	0.35	0.53	0.72	19259	0.35	0.54	0.73	21412
Fertilization intensity (log.)	0.19	0.28	0.36	20424	0.19	0.28	0.36	26251
ϕ	4079.13	5948.07	8898.77	17503	4176.99	6008.15	8956.41	20094
Measurement error σ	80.51	85.80	91.64	32550	80.42	85.73	91.62	33094
Bayes R²								
R ² Δ richness 1st year	0.03	0.10	0.20		0.29	0.41	0.51	
R ² Δ richness 5th year	0.13	0.25	0.37		0.26	0.39	0.49	
R ² productivity	0.30	0.44	0.54		0.30	0.44	0.54	

Table S3: Direct and indirect land-use and region effects on Δ richness, i.e. the difference in plant species richness between the respective treatment and the control, including all species. Δ richness of sown species and all species did not differ on the seeding only treatment in either year (see Table S2 above). On the seeding and disturbance treatment, mean Δ richness of all species is almost four species higher than sown species' Δ richness in the first year (ALB region Intercept 1st year here: median 9.84, sown species Δ richness: median 6.10; similar pattern for HAI and SCH region effects), which indicates that ruderal species from the soil seed bank contributed considerably to initial increases in species richness. In the 5th year, Δ richness of sown or all species only differed slightly (ALB region intercept and HAI and SCH region effects), which implies that ruderal species have disappeared and mostly sown species have established. Given here are the mean and the 90% credible interval and effective sample size of the posterior samples. 90% credible intervals that do not overlap zero are highlighted in bold. R-hat values <1.01 for all parameters indicated chain convergence.

	Seeding only				Seeding and disturbance			
	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}
Δ richness 1st year								
Intercept	0.00	0.98	1.96	44654	8.44	9.84	11.21	43037
Region HAI	-2.56	-0.18	2.24	37226	-7.15	-3.85	-0.50	34893
Region SCH	-3.22	-0.56	2.10	25630	-6.16	-2.53	1.12	27210
Mowing intensity	-2.17	-0.45	1.28	22062	-0.81	1.54	3.92	22043
Grazing intensity (log.)	-1.97	-0.35	1.27	24479	-0.89	1.33	3.61	22372
Productivity (log.)	-0.91	0.46	1.78	19167	-1.12	0.66	2.46	21701
σ	4.39	5.05	5.87	35308	6.17	7.07	8.22	31361
Δ richness 5th year								
Intercept	2.25	3.27	4.30	46055	7.52	8.77	10.01	42797
Region HAI	-0.26	2.28	4.80	37137	1.47	4.62	7.70	31854
Region SCH	-2.48	0.29	3.17	28036	-5.27	-1.90	1.50	26258
Mowing intensity	-2.15	-0.31	1.51	23126	-3.17	-0.98	1.24	22831
Grazing intensity (log.)	-2.05	-0.34	1.36	25523	-2.33	-0.24	1.85	23697
Δ richness 1st year	0.08	0.30	0.52	43966	0.09	0.28	0.46	34775
Productivity (log.)	-2.13	-0.68	0.75	20007	-3.57	-1.90	-0.25	21733
σ	4.64	5.34	6.21	30723	5.64	6.48	7.53	29891
Productivity								
Intercept	4.68	4.86	5.04	23000	4.67	4.86	5.04	19956
Region HAI	-0.28	-0.09	0.10	27426	-0.28	-0.09	0.10	25284
Region SCH	0.34	0.53	0.71	23791	0.35	0.53	0.72	21182
Fertilization intensity (log.)	0.20	0.28	0.36	25855	0.19	0.28	0.36	23222
ϕ	4114.32	5929.69	8758.51	20466	4137.03	5977.57	8857.00	18287
Measurement error σ	80.50	85.78	91.67	33319	80.46	85.74	91.72	34361
Bayes R²								
R ² Δ richness 1st year	0.02	0.07	0.15		0.04	0.13	0.23	
R ² Δ richness 5th year	0.08	0.17	0.28		0.19	0.31	0.42	
R ² productivity	0.30	0.44	0.54		0.30	0.44	0.54	

S4.4 Model diagnostics

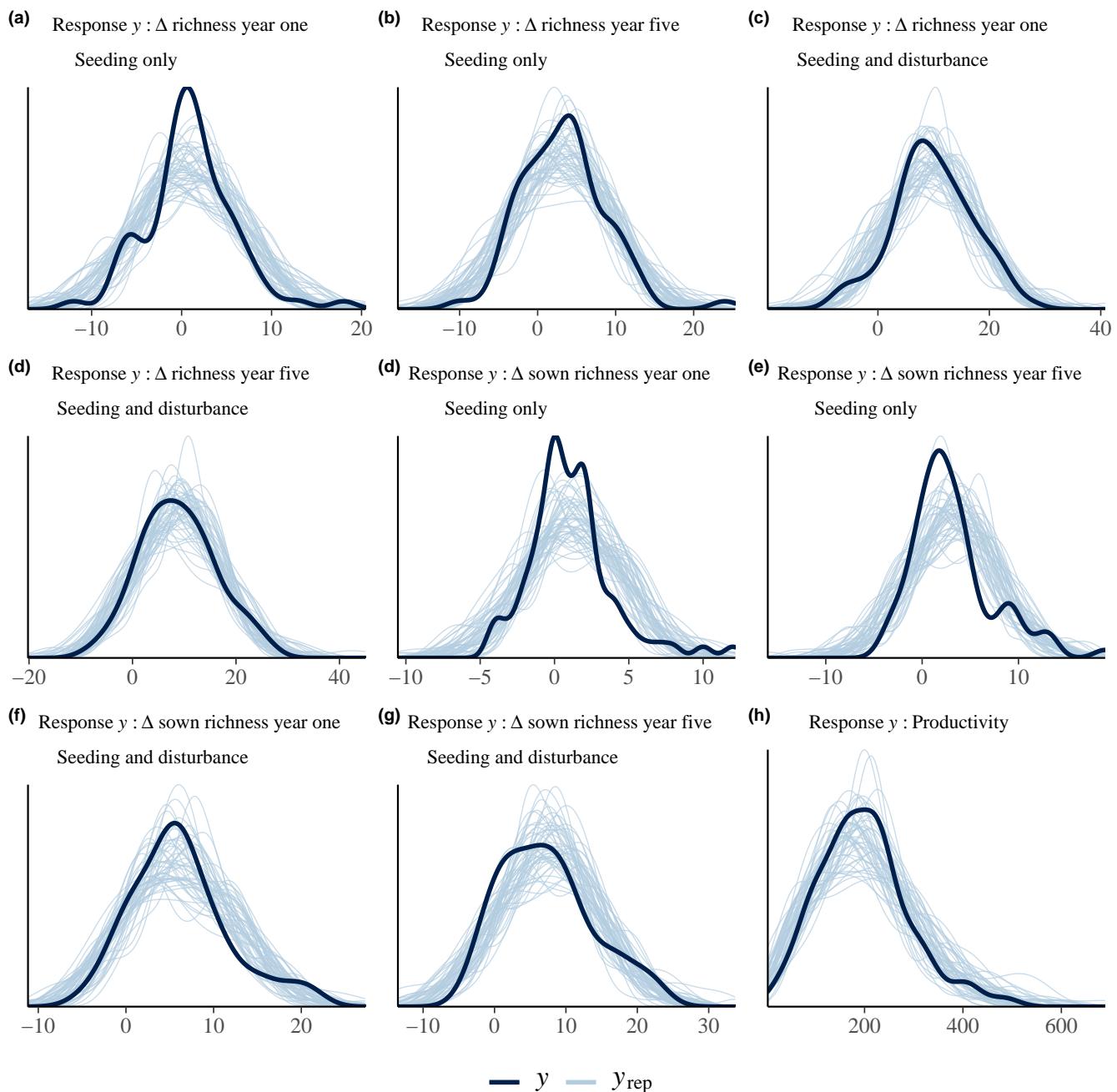


Figure S5: Kernel density estimates of observations (y) and 50 draws from the (y_{rep}) posterior predictive distribution for Δ richness in (a) the first and (b) fifth year on the seeding only and (c, d) seeding and disturbance treatment. (d) to (g) refer to the same models with sown species Δ richness as response y .

S5 Plant functional trait effects on establishment

S5.1 Model formulas

$Establishment\ success_i \sim \text{Bernoulli}(\mu_i)$, with

$$\begin{aligned} \text{logit}(\mu_i) = & \alpha \\ & + \beta_1 * \text{Low seeding density}_{i[j]} \\ & + \beta_2 * \text{High seeding density}_{i[j]} \\ & + \beta_3 * \log(\text{Height}_{i[j]}) \\ & + \beta_4 * \log(\text{Seed mass}_{i[j]}) \\ & + \beta_5 * \text{SLA}_{i[j]} \\ & + \beta_6 * \log(\text{Productivity}_{i[k]}) \\ & + \beta_7 * \log(\text{Productivity}_{i[k]}) * \log(\text{Height}_{i[j]}) \\ & + \beta_8 * \log(\text{Productivity}_{i[k]}) * \log(\text{Seed mass}_{i[j]}) \\ & + \beta_9 * \log(\text{Productivity}_{i[k]}) * \text{SLA}_{i[j]} \\ & + \text{Species}_{i[j]} + \text{Grassland}_{i[k]} \end{aligned} \quad (11)$$

$$\text{Species}_j \sim \text{Normal}(0, \sigma_{\text{Species}})$$

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

$$\text{Biomass}_{l[k]} \sim \text{Normal}(\text{Productivity}_k, \sigma_{\text{error}}) \quad (12)$$

Priors for establishment model (11):

$$\begin{aligned} \alpha & \sim \text{StudentT}(\nu = 3, \mu = 3, \sigma = 10) \\ \beta & \sim \text{Normal}(\mu = 0, \sigma = 5) \\ \sigma_{\text{species}} & \sim \text{StudentT}(\nu = 3, \mu = 3, \sigma = 10), \text{ constrained to be positive} \\ \sigma_{\text{grassland}} & \sim \text{StudentT}(\nu = 3, \mu = 3, \sigma = 10), \text{ constrained to be positive} \end{aligned} \quad (13)$$

Priors for productivity measurement error model (12):

$$\begin{aligned} \text{Productivity}_k & \sim \text{Normal}(\mu = \text{GrasslandMean}_k, \sigma = \text{GrasslandSD}_k) \\ \sigma & \sim \text{Cauchy}(\mu = 0, \sigma = 150), \text{ constrained to be positive,} \end{aligned} \quad (14)$$

We coded $Establishment\ success_i$ as binary and assumed successful establishment if the sown species has been recorded on the respective seeding treatment in the 5th year of the experiment. $\text{Low seeding density}_{i[j]}$ and $\text{High seeding density}_{i[j]}$ are the dummy-coded seeding densities of species j and depended on seed mass (see Methods). $\text{Height}_{i[j]}$, $\text{Seedmass}_{i[j]}$ and $\text{Specific leaf area}_{i[j]}$ (from the LEDA Traitbase, Kleyer et al., 2008), $\text{Productivity}_{i[k]}$ and interactions of traits with productivity were used as predictors. We included varying intercepts for species j ($\text{Species}_{i[j]}$) and grassland k ($\text{Grassland}_{i[k]}$). Productivity_k was again modelled as latent as in the models on land-use effects on the number of established sown species.

grazing intensity (in livestock unit * grazing days ha^{-1}), Mowing_i the mean number of cuts per year and Fertilization_i is the mean amount of fertilizer applied ($\text{kg Nitrogen ha}^{-1}$). Region_{HAI} and Region_{SCH} are dummy variables for the region, with Region_{ALB} as the reference level.

$Biomass_{i,j}$ is the harvested biomass (g m^{-2}) 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. All predictors were scaled to zero mean and unit SD to make effect sizes comparable.

We fitted models with Δ richness of total species richness (i.e., species richness including species which were not sown, such as ruderal species) using identical model specifications.

S5.2 Predictor variable distributions

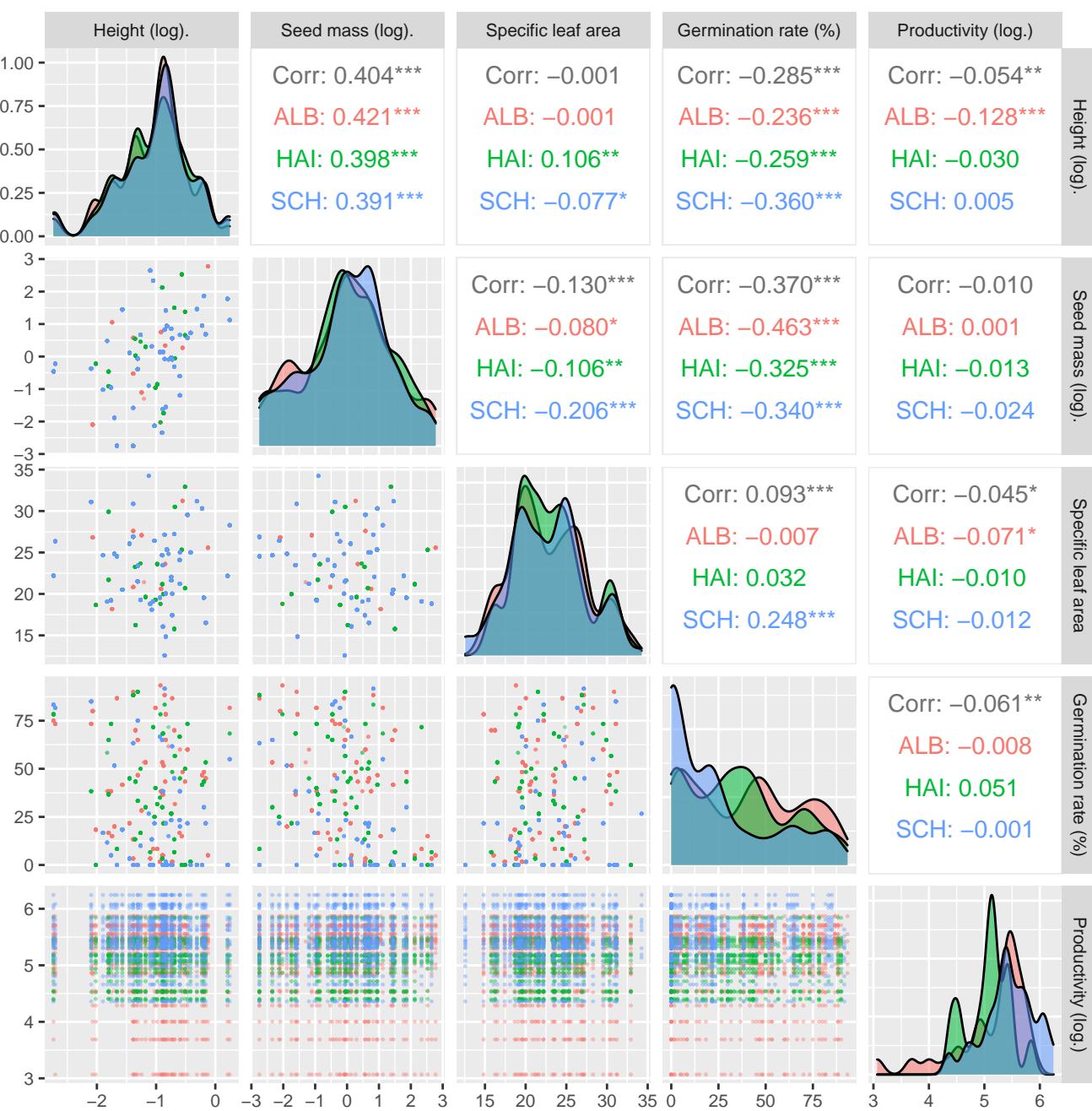


Figure S6: Distribution (diagonal), pairwise scatterplots (lower panels) and correlations (upper panels) of traits, germination rates (not used in the analyses) and productivity among the three regions. Plant height (in meter), seed mass (in mg) and productivity (in aboveground biomass g m^{-2}) were log-transformed as used in the models on trait and trait-productivity effects on species establishment

S5.3 Model diagnostics

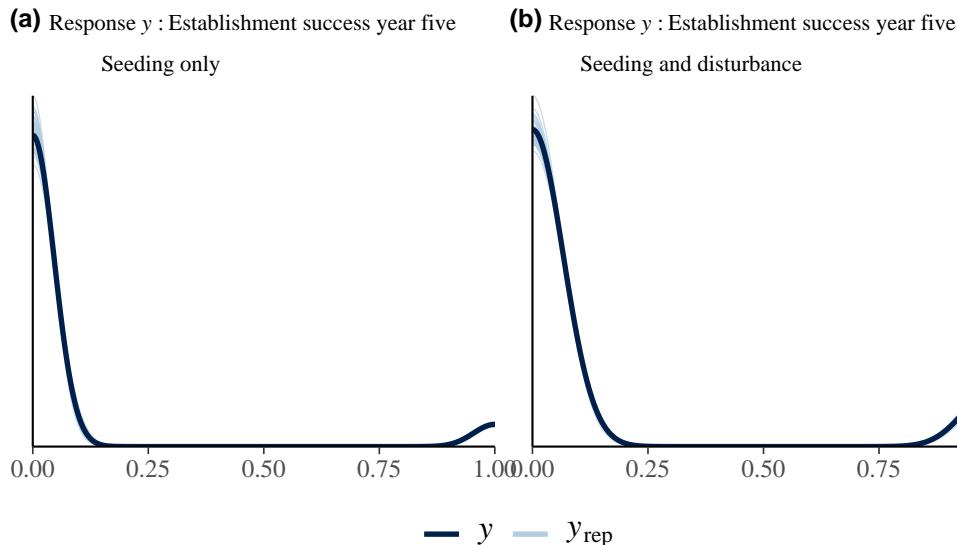


Figure S7: Kernel density estimates of observations (y) and 50 draws from the (y_{rep}) posterior predictive distribution for establishment success of plant species on (a) the seeding only and (b) the seeding and disturbance treatment.

S5.4 Parameter credible intervals

Table S4: Effects of traits, productivity and trait-productivity 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 and effective sample size 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. Credible intervals which do not overlap zero are shown in bold.

	Seeding only				Seeding and disturbance			
	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}
Intercept	-4.71	-4.06	-3.49	4061	-2.98	-2.54	-2.14	4430
Height (log.)	-2.44	-0.80	0.88	6354	-2.04	-0.97	0.05	7691
Seed mass (log.)	-0.86	0.81	2.50	6326	-1.80	-0.63	0.47	6648
SLA	-4.01	-2.14	-0.41	5121	-3.66	-2.51	-1.46	5700
Low seeding density	-1.14	1.08	3.32	6765	-1.87	-0.01	1.86	7470
High seeding density	0.81	1.83	2.96	4381	1.22	2.03	2.90	3945
Productivity (log.)	-2.62	-1.43	-0.25	4503	-2.60	-1.87	-1.15	5270
Height*Productivity	-0.86	0.84	2.48	6734	-0.09	0.93	1.99	8763
Seed mass*Productivity	-1.60	0.02	1.66	7213	0.70	1.75	2.89	8378
SLA*Productivity	0.22	2.21	4.32	5269	1.63	2.81	4.07	6307
SD Grassland	1.43	1.79	2.27	4877	1.09	1.34	1.63	5082
SD Species	1.27	1.67	2.19	4417	1.11	1.38	1.73	5194
σ Productiviy	80.58	85.87	91.67	17136	80.52	85.80	91.54	23675
R^2_{cond}	0.27	0.45	0.49		0.36	0.42	0.44	
R^2_{marg}	0.03	0.23	0.39		0.15	0.27	0.33	

S5.5 Model comparison of trait effects on establishment with grazing- and mowing-trait interactions

To investigate whether additional trait-environment interactions, i.e. interactions with grazing and mowing, influenced establishment, we modelled establishment with additional i) grazing and grazing-trait interactions, ii) grazing and grazing-trait interactions and iii) both grazing- and mowing-trait interactions as predictors. We used leave-one-out cross-validation (LOO) to compare model performances using the *loo* package (Vehtari, Gabry, Yao, & Gelman, 2020; Vehtari, Gelman, & Gabry, 2017).

The grazing- and mowing-trait interactions alone have weak effects on the establishment of sown species in both seeding treatments (Tables S5 and S6). However, for the seeding only treatment the model including all productivity-, grazing- and mowing-trait interactions show additional positive effects of mowing and grazing intensity as well as a negative SLA*grazing interaction. Despite, based on the LOO expected log pointwise predictive density for a new dataset (elpd_{LOO}), we assume the predictive performance of models with grazing- and/or mowing-trait interactions to be equivalent to the predictive performance of the ‘simplest’ model with only productivity-trait interactions (Table S7). We therefore only report the results of the productivity-trait model in the main text to avoid the complex interpretation of both grazing- and mowing-trait interactions in the presence of productivity-trait interactions.

Table S5: Effects of traits, productivity and trait-productivity interactions on the establishment success of sown species on the seeding only treatment. Establishment in the fifth year of the experiment was modelled exactly as for trait-productivity interactions only, but with additional grazing-, mowing- and grazing- and mowing-trait interactions. Given here are the mean and the 90% credible interval and effective sample size 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 and mowing frequency were log-transformed and scaled to unit SD to compare effect sizes. Varying intercepts for species and grassland were included. Credible intervals which do not overlap zero are shown in bold.

	plus Grazing				plus Mowing				plus Grazing and Mowing			
	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}
Intercept	-4.81	-4.14	-3.55	4891	-4.78	-4.10	-3.51	4552	-4.83	-4.15	-3.57	6587
High seeding density	0.76	1.84	3.02	4989	0.82	1.85	3.03	4620	0.81	1.87	3.02	7194
Low seeding density	-1.26	1.07	3.40	6890	-1.24	1.03	3.36	6562	-1.26	1.05	3.41	10224
Height (log.)	-2.75	-1.03	0.68	7325	-2.48	-0.83	0.85	6651	-2.96	-1.23	0.51	10025
Seed mass (log.)	-1.06	0.68	2.39	7074	-0.97	0.76	2.49	6527	-1.01	0.80	2.56	10448
SLA	-3.95	-2.06	-0.28	5481	-4.13	-2.25	-0.48	5526	-3.74	-1.82	-0.01	8486
Productivity (log.)	-2.72	-1.50	-0.29	5063	-2.77	-1.53	-0.34	4681	-3.13	-1.85	-0.59	6991
Height*Productivity	-0.83	0.88	2.61	7719	-0.85	0.90	2.61	7024	-1.14	0.68	2.46	9846
Seed mass*Productivity	-1.59	0.03	1.70	7751	-1.45	0.27	2.01	7502	-1.44	0.28	2.07	11051
SLA*Productivity	0.35	2.36	4.52	5717	0.33	2.37	4.52	5702	0.74	2.85	5.07	7943
Grazing (log.)	-0.36	0.81	1.99	8087					0.52	2.25	4.01	7445
Height*Grazing	-0.05	0.14	0.33	14769					-0.02	0.25	0.52	12169
Seed mass*Grazing	-0.11	0.08	0.28	15627					-0.30	-0.02	0.26	13754
SLA*Grazing	-0.34	-0.14	0.06	10722					-0.65	-0.35	-0.05	9511
Mowing					-0.80	0.30	1.40	7277	0.26	1.90	3.60	7417
Height*Mowing					-0.19	-0.02	0.15	15704	-0.10	0.16	0.41	13207
Seed mass*Mowing					-0.30	-0.12	0.06	15551	-0.39	-0.14	0.11	13786
SLA*Mowing					-0.20	-0.02	0.16	10187	-0.55	-0.27	0.00	9653
SD Grassland	1.47	1.85	2.34	4354	1.46	1.83	2.33	4816	1.48	1.88	2.40	5681
SD Species	1.30	1.71	2.25	4508	1.29	1.70	2.23	4924	1.30	1.72	2.25	5435
σ Productivity	80.60	85.84	91.64	18868	80.51	85.79	91.60	18871	80.63	85.80	91.66	22884

Table S6: Effects of traits, productivity and trait-productivity interactions on the establishment success of sown species on the seeding and disturbance treatment. Establishment in the fifth year of the experiment was modelled exactly as for trait-productivity interactions only, but with additional grazing-, mowing- and grazing- and mowing-trait interactions. Given here are the mean and the 90% credible interval and effective sample size 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 and mowing frequency were log-transformed and scaled to unit SD to compare effect sizes. Varying intercepts for species and grassland were included. Credible intervals which do not overlap zero are shown in bold.

	plus Grazing				plus Mowing				plus Grazing and Mowing			
	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}
Intercept	-3.00	-2.55	-2.13	3938	-3.00	-2.55	-2.13	3827	-3.02	-2.57	-2.16	4042
High seeding density	1.23	2.04	2.90	4295	1.21	2.03	2.91	4194	1.19	2.04	2.92	4154
Low seeding density	-1.84	0.01	1.90	7076	-1.86	0.02	1.86	7036	-1.86	0.04	1.96	7294
Height (log.)	-2.10	-1.00	0.05	6344	-2.09	-1.01	0.03	6094	-2.10	-0.98	0.10	7339
Seed mass (log.)	-1.96	-0.69	0.47	5850	-1.70	-0.51	0.60	5560	-1.99	-0.76	0.43	6159
SLA	-3.76	-2.54	-1.47	5800	-3.73	-2.55	-1.49	5831	-3.78	-2.56	-1.45	6099
Productivity (log.)	-2.65	-1.89	-1.17	5593	-2.74	-1.94	-1.18	5102	-2.91	-2.07	-1.28	5314
Height*Productivity	-0.08	0.93	2.01	7456	-0.07	1.02	2.13	6618	-0.08	1.04	2.22	7784
Seed mass*Productivity	0.74	1.79	2.97	7294	0.40	1.51	2.72	6519	0.08	1.26	2.51	7159
SLA*Productivity	1.67	2.83	4.13	6513	1.71	2.93	4.27	5875	1.78	3.07	4.49	5926
Grazing (log.)	-0.78	0.04	0.87	7654					-0.67	0.57	1.81	5614
Height*Grazing	-0.12	0.01	0.14	15131					-0.23	-0.03	0.18	10244
Seed mass*Grazing	-0.13	0.02	0.17	14196					-0.03	0.20	0.42	10168
SLA*Grazing	-0.13	0.01	0.15	10816					-0.25	-0.05	0.16	6918
Mowing					-0.57	0.24	1.04	6016	-0.54	0.66	1.86	5219
Height*Mowing					-0.16	-0.03	0.10	14017	-0.23	-0.05	0.14	9304
Seed mass*Mowing					-0.06	0.09	0.23	12564	0.01	0.22	0.44	9841
SLA*Mowing					-0.18	-0.04	0.09	8663	-0.27	-0.08	0.12	6538
SD Grassland	1.11	1.36	1.68	5303	1.11	1.36	1.67	4999	1.12	1.37	1.69	5258
SD Species	1.11	1.39	1.73	5393	1.11	1.39	1.74	5007	1.12	1.40	1.75	5150
σ Productivity	80.49	85.83	91.71	19947	80.45	85.80	91.71	17501	80.66	85.86	91.68	16840

Table S7: Comparison of sown species' establishment models with additional grazing- and mowing-trait interactions based on leave-one-out cross-validation. We used the expected leave-one-out prediction errors (which decrease with the expected log pointwise predictive density for a new dataset, elpd_{LOO}) to select the preferred model.

	elpd _{LOO}	SE(elpd _{LOO})	elpd _{diff}	SE(elpd _{diff})
Seeding only				
No grazing-/mowing-interactions	-505.41	30.49	0.00	0.00
Grazing-interactions	-505.61	30.70	-0.21	2.21
Mowing-interactions	-508.02	30.86	-2.62	1.46
Grazing- and mowing-interactions	-507.87	30.88	-2.46	2.75
Seeding and disturbance				
No grazing-/mowing-interactions	-853.37	31.59	0.00	0.00
Grazing-interactions	-856.30	31.78	-2.93	0.57
Mowing-interactions	-855.94	31.68	-2.57	1.29
Grazing- and mowing-interactions	-857.86	31.85	-4.49	2.33

S6 Effects of region and resident species richness on Δ richness

To test how Δ richness relates to the resident species richness of the same site, we modelled Δ richness with Gaussian errors as a function of region and resident species richness, which we log-transformed and scaled to unit SD. We specified weakly informative normal priors and default vague priors for the intercept. Increased Δ richness was related to higher resident species richness in the fifth year in both, seeding only and seeding and disturbance, treatments (Fig. S8, Table S8). 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.

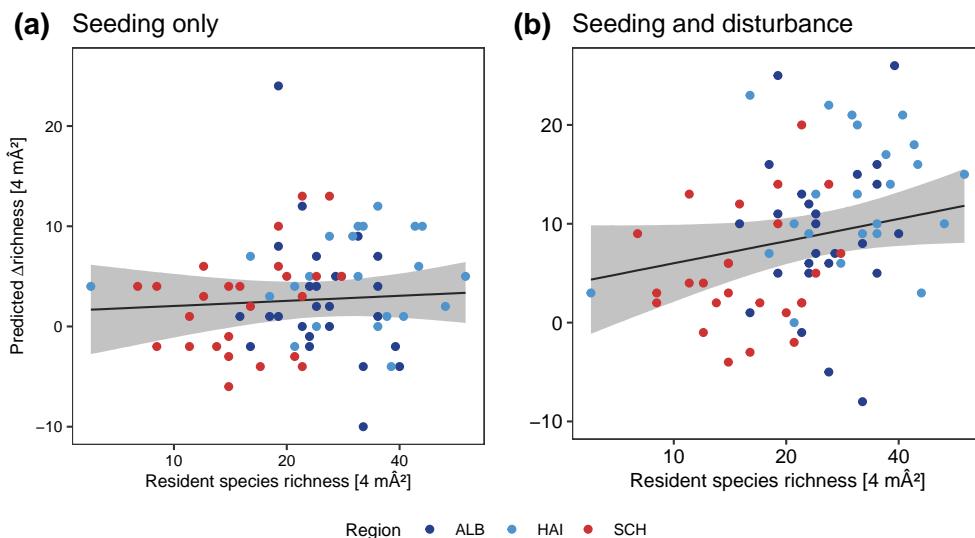


Figure S8: Conditional effect of resident species richness on Δ richness after five years in a) the seeding and b) the seeding and disturbance treatment. Lines refer to the predicted median and 90% credible intervals of Δ richness, conditioned on the region Alb (see Table S8 for details).

Table S8: Effects of region and resident species richness on Δ richness. Given here are the mean and the 90% credible interval and effective sample size of the posterior samples. Δ richness in the fifth year was modelled as a function of region and resident species richness (log-transformed and scaled to unit SD) in the same year. Credible intervals which do not overlap zero are shown in bold.

	Seeding only				Seeding and disturbance			
	5 %	50 %	95 %	N _{eff}	5 %	50 %	95 %	N _{eff}
Intercept (region ALB, centred predictor)	-8.95	0.37	9.67	14809	-12.88	-1.44	10.01	14164
Resident richness (log.)	-2.09	0.72	3.57	15566	-0.25	3.26	6.71	15265
Region HAI	-0.55	2.04	4.60	17369	-0.14	3.02	6.20	16251
Region SCH	-2.80	0.10	2.98	14315	-5.67	-2.16	1.35	13520
σ	4.77	5.44	6.32		5.93	6.78	7.86	
R^2	0.01	0.07	0.16		0.09	0.20	0.32	

S7 Cover of bare soil in relation to grazing, mowing and productivity

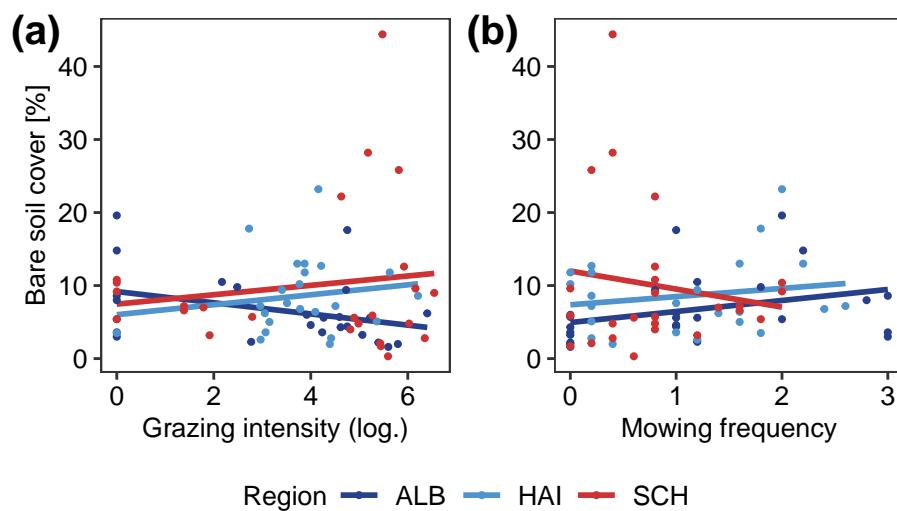


Figure S9: Visual estimates of bare soil cover on the control in relation to (a) grazing and (b) mowing intensities (averaged over the five years of study) as used as predictors in the analyses. Bare soil cover is only weakly associated to grazing and mowing. Lines denote linear model fits for each region separately.

S8 Establishment rates of sown plant species

Table S9: Establishment rates of sown plant species 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. We assumed sown species to have successfully established if they were observed in the fifth year of the experiment.

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

Table S9: Establishment rates of sown plant species in the seeding only treatment (*continued*)

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

Table S10: Establishment rates of sown plant species 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. We assumed sown species to have successfully established if they were observed in the fifth year of the experiment.

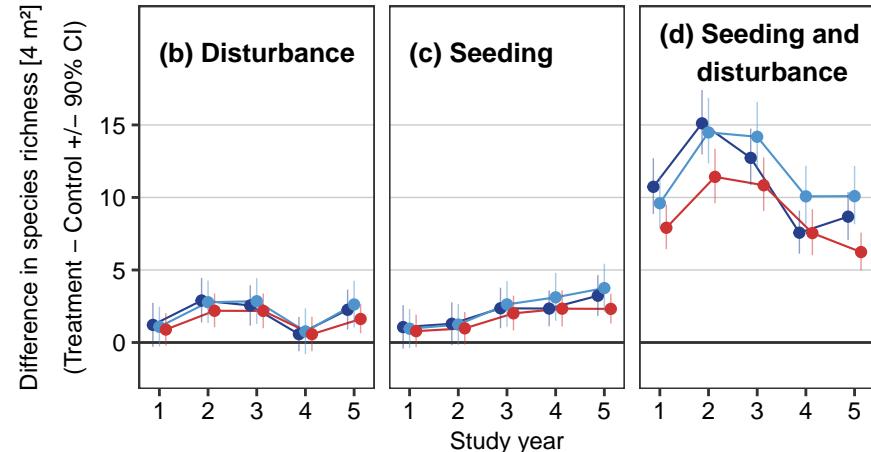
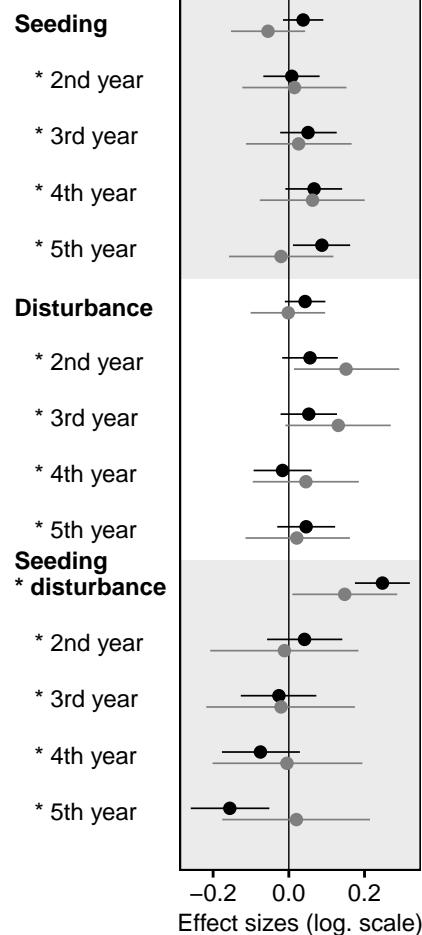
	Establishment success %	ALB		HAI		SCH	
		No. newly sown	No. established	No. newly sown	No. established	No. newly sown	No. established
Non-legume herbs							
<i>Achillea millefolium</i>	67	7	6	5	2		
<i>Agrimonia eupatoria</i>	8	17	2	7	2	25	0
<i>Anthriscus sylvestris</i>	0	8	0	12	0	20	0
<i>Betonica officinalis</i>	17	24	4	23	4		
<i>Campanula rotundifolia</i>	0	16	0	23	0	25	0
<i>Cardamine pratensis</i>	5	20	1				
<i>Centaurea jacea</i>	22	24	3	15	10	25	1
<i>Centaurea scabiosa</i>	25	25	4	23	9	25	5
<i>Cichorium intybus</i>	5	25	0	10	1	21	2
<i>Cirsium oleraceum</i>	2	22	1	23	0	21	0
<i>Clinopodium vulgare</i>	20	25	0	21	9		
<i>Crepis biennis</i>	42	12	5				
<i>Daucus carota</i>	12	18	2	6	1	18	2
<i>Dianthus carthusianorum</i>	43	24	10	22	10		
<i>Falcaria vulgaris</i>	0					24	0
<i>Galium mollugo</i>	50	3	2	9	5	14	6
<i>Geranium pratense</i>	61	13	6	18	13		
<i>Heracleum sphondylium</i>	17	10	0	18	1	18	7
<i>Hypericum perforatum</i>	9	19	3	16	0	23	2
<i>Hypochaeris radicata</i>	16	19	6	23	2	22	2
<i>Knautia arvensis</i>	20	16	8			24	0
<i>Leontodon autumnalis</i>	23	21	5			14	3
<i>Leontodon hispidus</i>	7	20	2	17	2	24	0
<i>Leucanthemum vulgare</i>	21	18	4	15	3		
<i>Linaria vulgaris</i>	17	25	5	22	3		
<i>Lychnis floscululi</i>	4	24	0	22	3	24	0
<i>Origanum vulgare</i>	15	24	8	23	0	24	3
<i>Pastinaca sativa</i>	8	25	2	12	1		
<i>Pimpinella major</i>	0			22	0	25	0
<i>Pimpinella saxifraga</i>	2	17	0			25	1
<i>Plantago lanceolata</i>	21	3	2	2	0	9	1
<i>Plantago media</i>	22	11	2	16	8	23	1
<i>Primula veris</i>	28	22	4	18	7		
<i>Prunella vulgaris</i>	6	25	0	19	3	25	1
<i>Ranunculus acris</i>	6	3	0	13	1		
<i>Ranunculus bulbosus</i>	14	14	2				
<i>Rumex acetosa</i>	41	6	1	16	8		
<i>Rumex acetosella</i>	5					20	1
<i>Salvia pratensis</i>	1	22	0	23	0	25	1
<i>Sanguisorba minor</i>	32	19	5	20	11	21	3
<i>Sanguisorba officinalis</i>	0					25	0
<i>Scabiosa columbaria</i>	4			22	0	23	2
<i>Silaum silaus</i>	0	25	0			24	0
<i>Silene latifolia</i>	9	25	1	23	2	20	3
<i>Silene vulgaris</i>	34	23	3	23	16	25	5
<i>Succisa pratensis</i>	0					25	0
<i>Thymus pulegioides</i>	10	18	1			24	3
<i>Tragopogon pratensis</i>	8	16	0	11	4	22	0
<i>Veronica chamaedrys</i>	10	6	1			14	1

Table S10: Establishment rates of sown plant species in the seeding and disturbance treatment (*continued*)

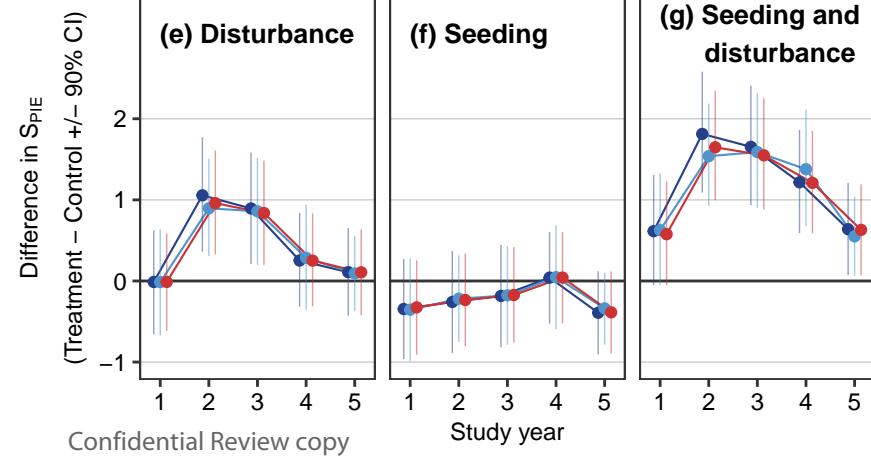
	Establishment success %	ALB		HAI		SCH	
		No. newly sown	No. established	No. newly sown	No. established	No. newly sown	No. established
<i>Veronica officinalis</i>	8	25	2				
Legumes							
<i>Lathyrus pratensis</i>	59	18	8	16	12		
<i>Lotus corniculatus</i>	8	13	1				
<i>Medicago lupulina</i>	7	14	1		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

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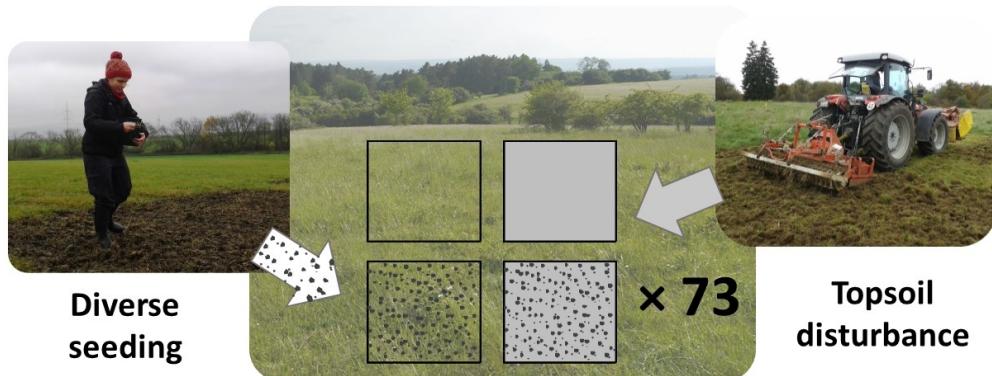
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● Species richness ● Spie

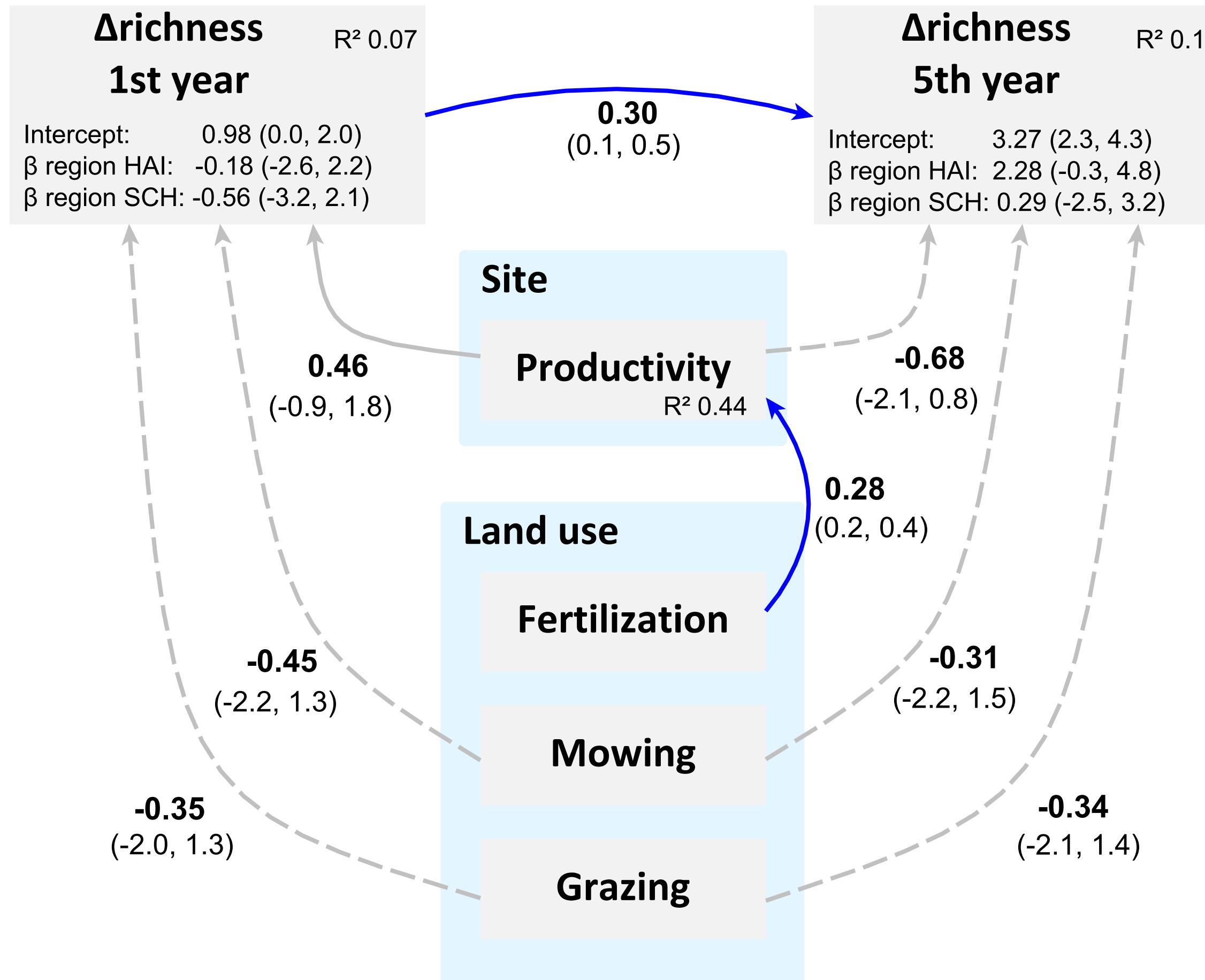
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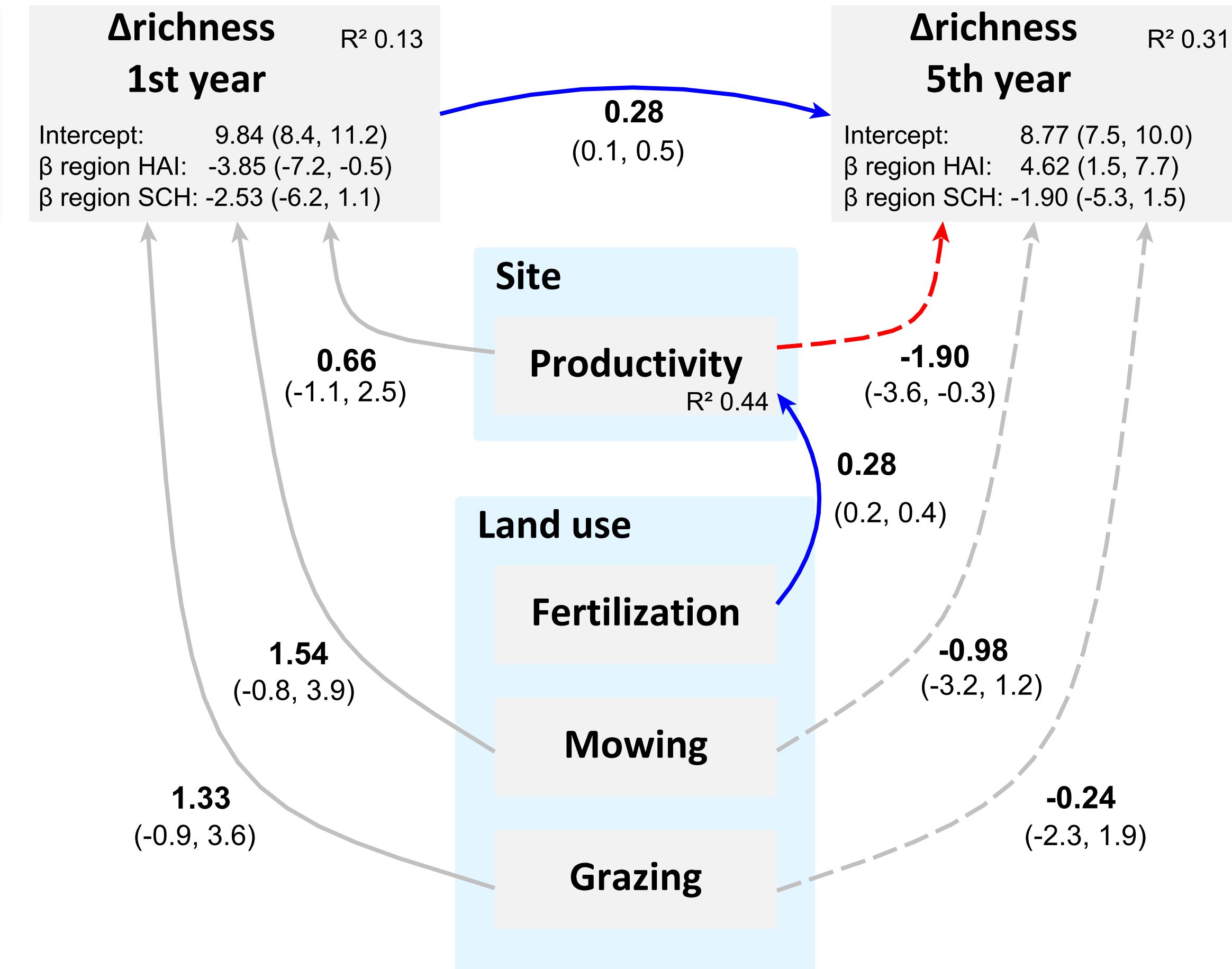
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Species richness

(a) Seeding only

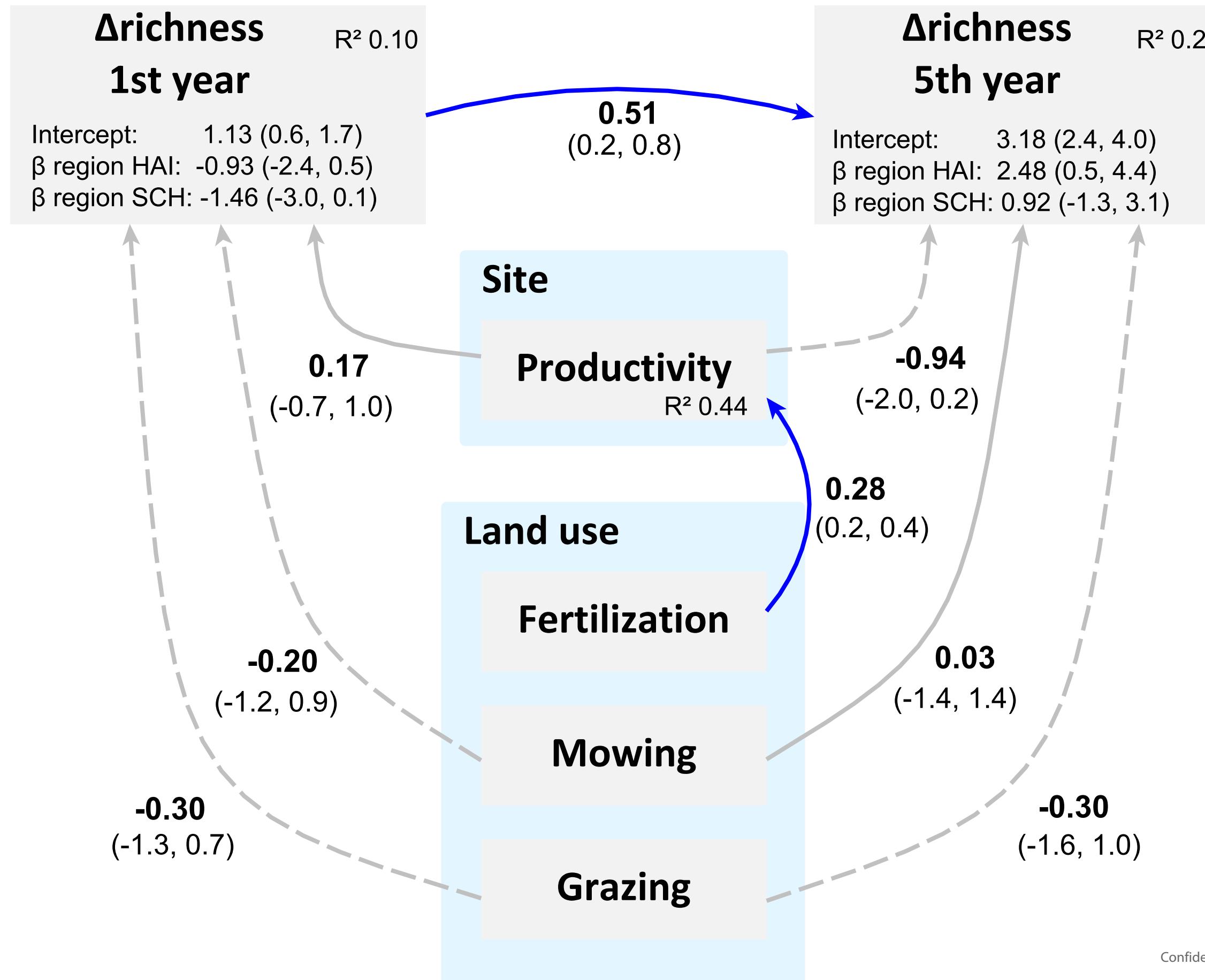


(b) Seeding and disturbance

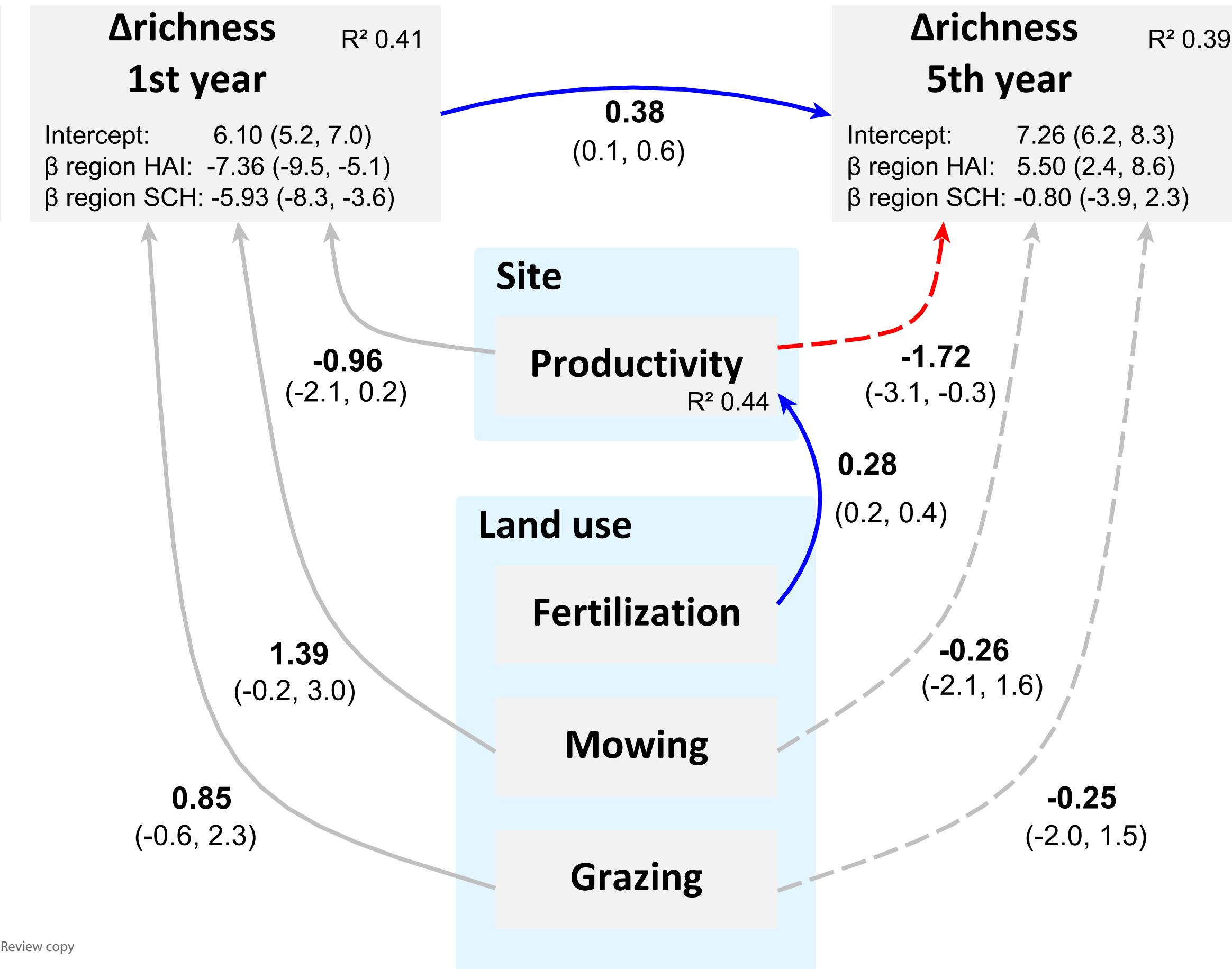


Species richness of sown species

(c) Seeding only

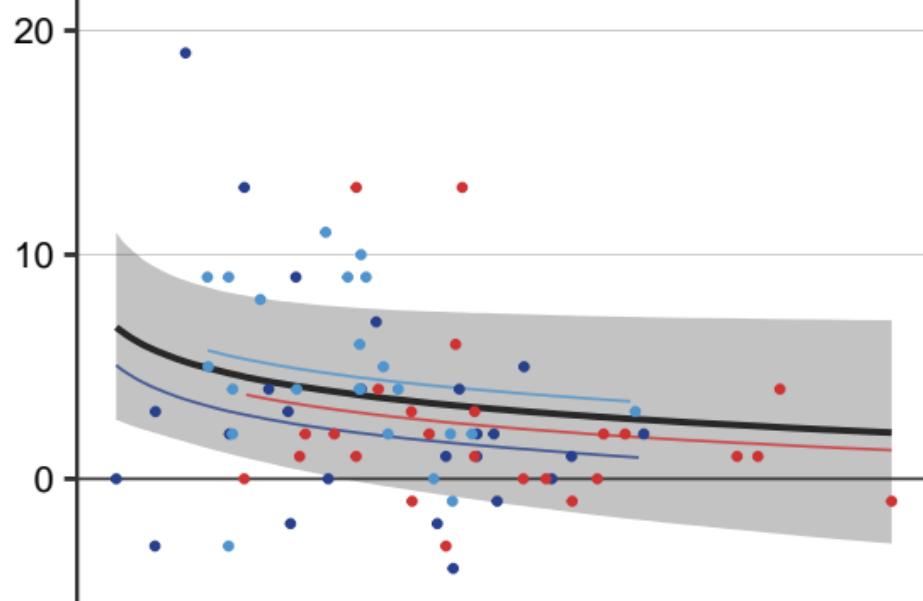


(d) Seeding and disturbance



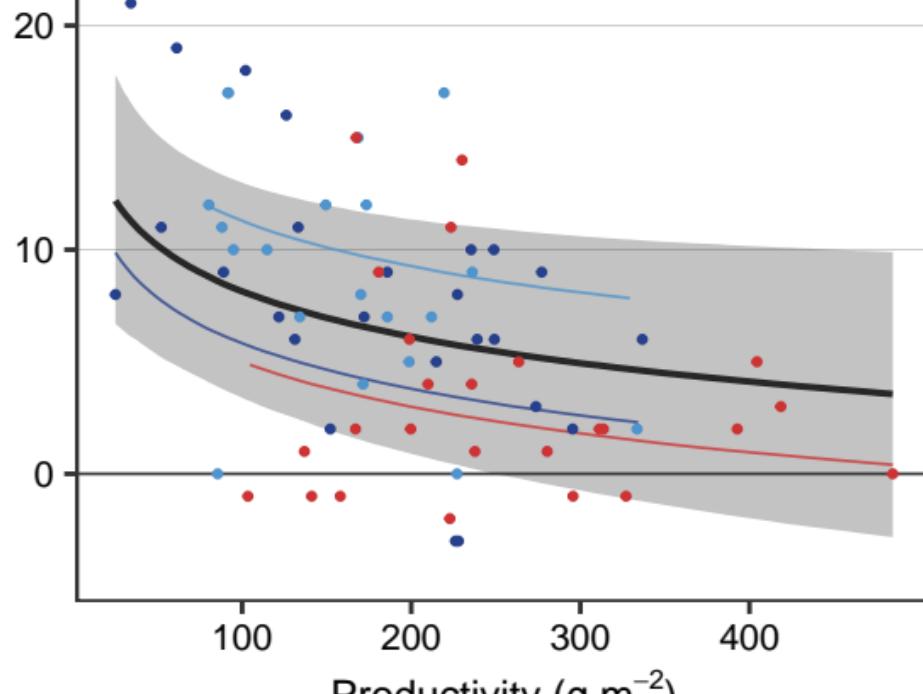
(a) Seeding

Sown species Δrichness 5th year



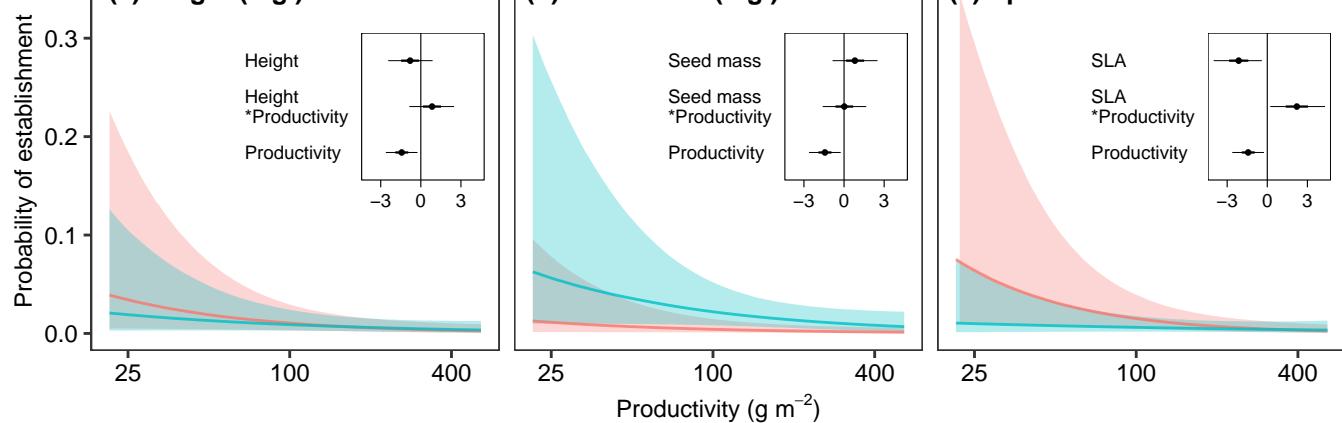
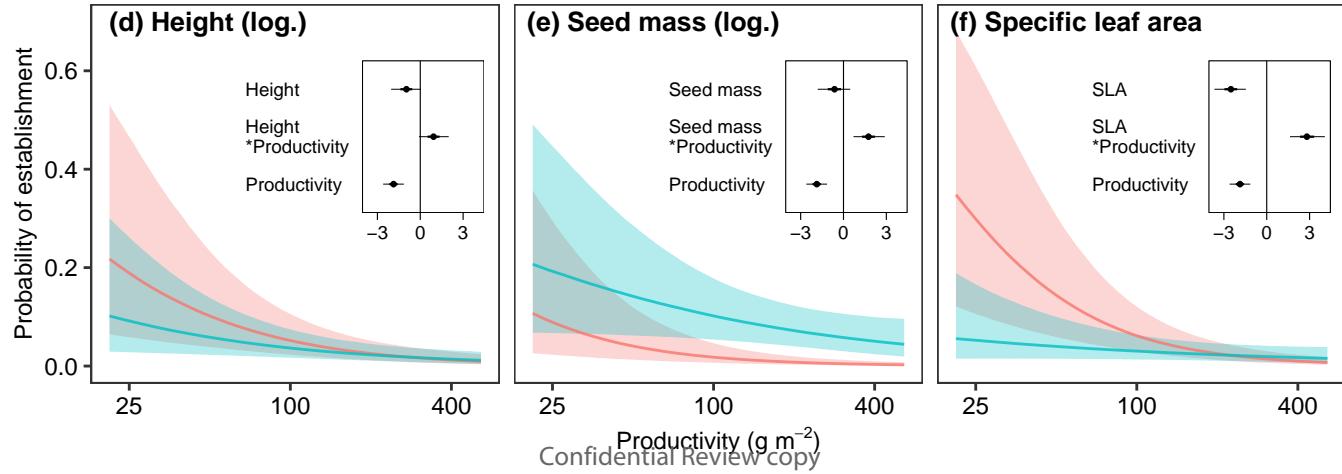
(b) Seeding and disturbance

Sown species Δrichness 5th year



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Region ALB HAI SCH

**Seeding and disturbance**

Trait value Mean – SD Mean + SD