



Recovery of ecosystem functions after experimental disturbance in 73 grasslands differing in land-use intensity, plant species richness and community composition

Journal Article

Author(s):

Schäfer, Deborah; Klaus, Valentin ; Kleinebecker, Till; Boeddinghaus, Runa S.; Hinderling, Judith; Kandeler, Ellen; Marhan, Sven; Nowak, Sascha; Sonnemann, Ilja; Wurst, Susanne; Fischer, Erich ; Hölzel, Norbert; Hamer, Ute; Prati, Daniel

Publication date:

2019-11

Permanent link:

<https://doi.org/10.3929/ethz-b-000372784>

Rights / license:

[In Copyright - Non-Commercial Use Permitted](#)

Originally published in:

Journal of Ecology 107(6), <https://doi.org/10.1111/1365-2745.13211>

1 **Recovery of ecosystem functions after experimental disturbance in 73 grasslands differing in land-**
2 **use intensity, plant species richness and community composition**

3 Deborah Schäfer^{1*}, Valentin H. Klaus^{2,3}, Till Kleinebecker^{2,4}, Runa S. Boeddinghaus⁵, Judith Hinderling¹,
4 Ellen Kandeler⁵, Sven Marhan⁵, Sascha Nowak⁷, Ilja Sonnemann⁶, Susanne Wurst⁶, Markus Fischer¹,
5 Norbert Hölzel², Ute Hamer², Daniel Prati¹

6

7 ¹ University of Bern, Institute of Plant Sciences, Altenbergrain 21, 3013 Bern, Switzerland

8 ² Münster University, Institute of Landscape Ecology, Heisenbergstr. 2, 48149 Münster, Germany

9 ³ Institute for Agricultural Sciences, ETH Zürich, Universitätstrasse 2, 8092 Zürich, Switzerland

10 ⁴ Giessen University, Institute of Landscape Ecology and Resources Management, Heinrich-Buff-Ring
11 26, 35392 Giessen, Germany

12 ⁵ University of Hohenheim, Institute of Soil Science and Land Evaluation, Department of Soil Biology,
13 Emil-Wolff Strasse 27, 70599 Stuttgart, Germany

14 ⁶ Freie Universität Berlin, Dahlem Centre of Plant Sciences, Berlin, Germany

15 ⁷ Münster University, MEET - Münster Electrochemical Energy Technology, Corrensstraße 46, 48149
16 Münster, Germany

17

18 *Corresponding author: deborah.schaefer@boga.unibe.ch

19

20

21

22

23

24

25

26 **Abstract**

- 27 1. Drivers of ecosystem stability have been a major topic in ecology for decades. Most studies
28 focused on the influence of species richness on ecosystem stability and found positive
29 diversity-stability relationships. However, land use and abiotic factors shape species richness
30 and functional composition of plant communities and may override species richness-stability
31 relations in managed grasslands.
- 32 2. We analysed the relative importance of land-use intensity (LUI), resident plant species
33 richness and functional composition on recovery of plant communities (plant species richness,
34 plant cover, above- and belowground biomass) and release of soil nutrients after a severe
35 mechanical disturbance. Experimental sward disturbance was applied on 73 grassland sites
36 along a LUI gradient in three German regions. We considered relative
37 ($\ln(\text{disturbance}/\text{control})$) and absolute ($\text{disturbance} - \text{control}$) treatment effects. Using
38 structural equation modelling, we disentangled direct effects of LUI and resident species
39 richness on recovery and indirect effects via changes in functional richness.
- 40 3. Community-weighted-mean traits rarely mattered for recovery or nutrient release, while
41 functional richness increased especially relative recovery of plant communities but also
42 relative release of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$. These effects increased with increasing resident plant
43 species richness and decreasing LUI. Next to these indirect influences of LUI and resident plant
44 species richness via functional community composition, grasslands of high compared with low
45 grasslands of low resident plant species richness, generally showed decreased recovery of
46 plant communities. In grasslands of high LUI, absolute recovery of some aspects of plant
47 communities was decreased. We did not find consistent differences between the relative
48 importance of the different drivers of recovery after the first and the second season. Overall,
49 Resident species richness seemed most important for relative recovery and less important for
50 absolute recovery, where direct effects of LUI were more common.

51 4. *Synthesis*: The stability of ecosystems in managed grasslands depends on more than species
52 richness. Thus, drivers that directly affect species richness and functional community
53 composition have to be considered when studying stability of real-world ecosystems. More
54 specifically, in managed grasslands, high resident species richness but also high LUI decreased
55 the stability of ecosystem functions, which was partially buffered by increases in functional
56 richness.

57 **Keywords:** agricultural grasslands, diversity-stability relationship, nutrient availability, plant
58 community, productivity, recovery, soil disturbance

59 **Introduction**

60 On the background of more frequent disturbances due to global changes (Easterling 2000), knowledge
61 on the characteristics of an ecosystem that will ensure the recovery of its functions, i.e. regain of
62 ecosystem functions equal to pre-disturbance levels, has significantly increased in importance (Kayler
63 et al., 2015). A quick recovery after disturbances safeguards ecosystem functions and ecosystem
64 services for human well-being. Studying the effects of disturbances on ecosystems and their functions
65 is therefore important for fundamental and applied ecological perspectives.

66 Species richness has been frequently suggested to increase stability, as defined by different concepts,
67 including the recovery of ecosystem functions (McCann, 2000; Isbell et al., 2015, DeBoeck et al., 2018),
68 as the presence of many species within a community increases the chances of having a species with
69 certain traits adapted to a specific disturbance (insurance hypothesis: Yachi & Loreau, 1999). Managed
70 grasslands are covering vast parts of the earth surface, are amongst the most species rich communities
71 worldwide and are providing many different ecosystem services (Wilson, Peet, Dengler, Pärtel, &
72 Palmer, 2012; Allan et al., 2015). Across natural ecosystems the influence of species richness on the
73 recovery of ecosystem functions could be confounded by environmental gradients, such as land-use
74 intensity. However such confounding effects are far less studied (Grman, Lau, Schoolmaster, & Gross,
75 2010; Yang et al., 2012; Hautier et al., 2014; Blüthgen et al., 2016). On the one hand, land-use intensity

76 may directly reduce recovery of ecosystem functions due to additional disturbances by removing
77 biomass via mowing or grazing (Vogel et al., 2012; Stampfli et al., 2018) or it could directly increase
78 recovery of ecosystem functions by adding nutrients via fertilization, which for example promotes
79 biomass regrowth after a disturbance (Loeser et al., 2007). On the other hand, high land-use intensity
80 reduces plant species richness (Socher et al., 2012; Allan et al., 2015; Hautier et al., 2014) and changes
81 the functional community composition and richness, which can have subsequent indirect effects on
82 recovery (Pakeman, 2011; Allan et al., 2015). Decreasing species richness and functional richness could
83 lead to negative indirect effects of high land-use intensity on the recovery of plant communities and
84 their ecosystem functions as described above. Then again, changes in the functional composition of
85 plant communities due to high land-use intensity, e.g. more exploitative species with faster re-growth
86 capacity (Pfestorf et al., 2013; Allan et al., 2015), could also lead to indirect positive effects of high
87 land-use intensity on recovery of plant communities and ecosystem functions. To understand the
88 potential for recovery of the ecosystem functions of managed grasslands after a disturbance, it is
89 critical to study the importance of land-use intensity, plant species richness and functional community
90 composition and to disentangle their direct and indirect effects.

91 Most studies analysed the effect of relatively weak disturbances like short drought periods (e.g. Frank
92 & McNaughton, 1991) or grazing (e.g. Hallett, Stein, & Suding, 2017), while far less studies considered
93 recovery after strong disturbances (DeBoeck et al., 2018) like severe droughts or mechanical
94 disturbances. After a severe disturbance, as they occur in agriculturally used grasslands, during
95 grassland renewal (European Communities, 2008) or due to the activity of wild boars (Massei & Genov,
96 2004), large parts of the plant community are completely disrupted. Here, plant community
97 characteristics, i.e. species richness and functional composition, might be less important for recovery
98 of ecosystem functions than after weak disturbances and land-use intensity and changes of abiotic
99 conditions like soil water content, likely play a more important role. The relative importance of
100 different drivers might therefore be very different for the recovery after severe disturbances
101 compared with recovery after weak disturbances (Dornelas, 2010; DeBoeck et al., 2018) and more

102 studies analysing recovery after severe disturbances are therefore needed to understand the role of
103 different drivers under these circumstances.

104 We assessed the relative importance of land-use intensity, resident species richness and functional
105 community composition on the recovery of plant communities and soil nutrient release. This was done
106 in 73 agricultural grasslands after a severe mechanical sward disturbance. We included several
107 ecosystem functions related to plant communities and nutrient release, to assess whether drivers
108 affect recovery generally or rather specifically for each ecosystem functioning. We also included soil
109 water content to account for possible influences of changed soil water conditions in the disturbed
110 soils. The grassland sites covered a wide gradient in plant species richness that coincided with a
111 gradient of land-use intensity commonly observed in Central European grasslands (Fischer et al.,
112 2010). This enabled us to study the interacting effects of plant species richness, land-use intensity and
113 functional community composition on the recovery of plant communities and nutrient release.

114 Previous work on this experiment has shown that sward disturbance increases cover of bare soil,
115 seedling species richness and number of seedlings directly after disturbance due to the activation of
116 the soil seed bank (Klaus et al. 2017) and release of nitrate (Klaus et al., 2018). In the present study,
117 we investigated how the disturbance effects and recovery of ecosystem functions are related to land-
118 use intensity, plant species richness and functional composition in the first and second season after
119 the sward disturbance and tested the following hypotheses:

- 120 1. Grasslands with high functional richness have faster recovery of their plant communities and
121 lower nutrient release than grassland with low functional richness.
- 122 2. Grasslands with high resident species richness have faster recovery of their plant communities
123 and lower nutrient release than grasslands with low resident species richness.
- 124 3. High land-use intensity directly increases recovery of plant communities and nutrient release
125 but indirectly decreases the recovery of plant communities and nutrient release via decreasing
126 resident species richness and functional richness.

127 **Materials and Methods**

128 *Study site*

129 Field work took place from 2014 until 2016 on 73 permanent agricultural grassland sites located in
130 three German regions, as part of the large-scale and long-term Biodiversity Exploratories project
131 (Fischer et al., 2010). The three different regions are the Schwäbische Alb (25 sites) in SW-Germany,
132 the Hainich-Dün (23 sites) in Central Germany and the Schorfheide-Chorin (25 sites) in NE-Germany.
133 Details on regional characteristics, including climate and soils, are given in Fischer et al. (2010). The
134 grassland sites were chosen along local land-use intensity gradients, which are comparable between
135 the different regions (Fischer et al., 2010; Blüthgen et al., 2012) and are typical for grassland
136 management in central Europe. The grasslands have been agriculturally used as grasslands at least
137 since 30 years (Fischer et al., 2010).

138 To determine the land-use intensity we gathered information from farmers with a standardized
139 questionnaire. We inquired the amount of fertilizer applied ($\text{kg nitrogen} \times \text{ha}^{-1} \times \text{yr}^{-1}$), the frequency of
140 mowing (number of cuts $\times \text{yr}^{-1}$) and the grazing intensity (number of livestock units \times grazing days \times
141 $\text{ha}^{-1} \times \text{yr}^{-1}$). Based on this data we calculated an index of land-use intensity (LUI) according to Blüthgen
142 et al. (2012) by extracting the square root of the sum of fertilization, grazing and mowing intensities
143 for each grassland after dividing each component by the respective mean for all plots in 2014.

144
$$LUI = \sqrt{\frac{\text{fertilizer}_{plot}}{\text{fertilizer}_{mean}} + \frac{\text{mowing}_{plot}}{\text{mowing}_{mean}} + \frac{\text{grazing}_{plot}}{\text{grazing}_{mean}}}$$

145 This resulted in a continuous gradient of the LUI index ranging from 0 to 3.5 (dimensionless). For
146 example, a very low LUI of 0.5 can be achieved through 30 days grazing by one livestock unit of cattle
147 $\text{ha}^{-1} \text{yr}^{-1}$, an intermediate LUI of 1.5 corresponds to a meadow which is mown twice and received 60
148 $\text{kg N ha}^{-1} \text{yr}^{-1}$, and a relatively high LUI of 3.0 corresponds to a meadow which is mown three times and
149 received 130 $\text{kg N ha}^{-1} \text{yr}^{-1}$. The grasslands additionally comprise a gradient of plant species richness,
150 which was measured for each grassland independently, in close proximity to the treatment on 4 m \times

151 4 m plots in May and June 2014 (Socher et al., 2012), hereafter referred to as resident plant species
152 richness. Both LUI and resident plant species richness were used as explanatory variables.

153 *Experimental design*

154 We conducted a field experiment on two 7 m × 7 m plots on each of the 73 agricultural grassland sites,
155 consisting of a control and a disturbance plot. The disturbance treatment consisted of an intensive
156 mechanical perturbation of the sward and the upper 10 cm of the soil with a rotary harrow
157 (Schwäbische Alb and Hainich-Dün) or a rotary cultivator (Schorfheide-Chorin) in October 2014, after
158 the regular grassland management practices on the sites had ended for this year. We chose different
159 methods for sward disturbance according to the methods typically used in the respective regions.
160 After disturbance (without any reseeding), the fragments of the plants, including tussocks and roots,
161 remained on the plots and the regular management by the farmers continued.

162 *Plant species richness and productivity*

163 In May and June 2015 and 2016, we recorded plant species richness on 2 m × 2 m in the treatment
164 plots in all grasslands and estimated the cover percentage of each species. For total plant cover we
165 summed the cover of all species. At the same time, we assessed productivity as aboveground and
166 belowground biomass. For aboveground biomass, we cut the plant biomass at 2 cm above ground on
167 four 50 cm × 50 cm plots on all treatment plots. Plant biomass was dried at 80 °C for 48 h and weighed
168 to the nearest gram. The four values per plot were then summed and given as g m⁻². In 2015, we
169 measured belowground biomass immediately after cutting the aboveground biomass. We took four
170 soil cores, from 0–10 cm depth with a diameter of 5.6 cm, per treatment plot and sieved the soil to
171 collect roots and stones > 2 mm. We washed the attached soil material from the roots and
172 subsequently dried all root fragments until constant weight at 60 °C (minimum 72 hours). We weighed
173 the dried roots and, as for aboveground biomass, transformed the belowground biomass to g m⁻² using
174 the diameter of the soil corer. Due to the very labour intensive methods required for taking root
175 biomass measurements we decided to measure them in the first season after the disturbance only,
176 where impact of the sward disturbance was expected to be most pronounced.

177 *Soil nutrients*

178 We used ion-exchange resin bags (Sibbesen, 1977; Skogley & Dobermann, 1996), i.e. nylon bags
179 containing anion/cation mixed-bed resin beads plus specific resin beads for anionic heavy metals and
180 phosphate (TerrAquat, Nürtingen, Germany), to measure nutrient availability in terms of nitrate (NO₃-
181 N), ammonium (NH₄-N), potassium (K) and phosphate (PO₄-P) concentrations in situ. Each resin bag
182 with a diameter of 5 cm contained 19.5 g dry resin. We installed a total of 438 bags, three replicates
183 with a minimum distance of 6 m in all treatment plots, at 20 cm depth four months after experimental
184 sward disturbance. We left the bags in the soil from March to early August 2015, approximately 145
185 days.

186 After removal, we stored the resin bags in a refrigerator. We extracted the nutrients for each bag
187 separately. With 100 ml 1M NaCl we extracted 15 g moist resin in two steps. In each step we used 50
188 ml, and shook it for 30 min before filtering it. We measured NH₄-N and NO₃-N concentrations with a
189 Continuous Flow Auto Analyser (Skalar Analytic GmbH, The Netherlands) and potassium (K)
190 concentrations with a Spectro ARCOS ICP-OES (Spectro Analytical Instruments, Kleve, Germany). After
191 applying a standard Fassel-type torch (inner diameter: 1.8 mm) in axial position for the elemental
192 determination we introduced the samples by a cross flow nebulizer and a Scott spray chamber. As
193 nebulizer gas we used argon with a flow rate of 0.8 L min⁻¹, as auxiliary plasma gas we used argon with
194 a flow rate of 0.85 L min⁻¹ and as cooling gas we used argon with a flow rate of 12.0 L min⁻¹. The radio
195 frequency was 1400 W and we selected the most sensitive wavelengths after. We measured samples
196 either directly or after diluting them 1:10 in ultra-pure water (Millipore Milli-Q system, Schwalbach,
197 Germany). We extracted PO₄-P in an additional 15 g sample of moist resin using 100 ml 0.5M H₂SO₄
198 and measured it following the same protocol as described above. We state all concentrations as mean
199 values per treatment plot in µg g⁻¹ (dry weight) resin. In four plots NO₃-N values were below detection
200 limit. As total absence of the respective nutrient is unlikely we set NO₃-N concentration values at 10
201 % of the lowest measured value. Due to the very labour intensive methods, we decided to measure

202 soil nutrients in the first season after the disturbance only, where impact of the sward disturbance
203 was expected to be most severe.

204 *Soil moisture*

205 To measure soil moisture in the disturbance plots we collected three soil cores of 2 cm diameter and
206 6 cm depth from each disturbance plot. We sampled all plots within a period of four weeks in April
207 and May 2015 and 2016. We pooled the samples per disturbance plot, removed stones and roots and
208 took a subsample of 5 g. We determined the water content as the difference in weight before and
209 after drying in a drying oven for 24 h at 105° C. Despite the high seasonal variation of soil moisture
210 commonly found, our soil moisture measurements between 2015 and 2016 were highly correlated
211 (Spearman $r = 0.76$, $p < 0.001$). We include soil moisture in our statistical analysis to control for
212 disturbance effects mediated by creating open soil and thereby reducing soil moisture.

213 *Trait data*

214 We used specific leaf area (SLA), the occurrence of a bud bank and lateral spread as species-specific
215 functional traits to assess functional composition of plant communities. Traits were derived from the
216 databases TRY (Kattge et al., 2011) and CLOPLA (Klimešová & Bello, 2009). In a pre-analysis SLA proved
217 to be almost identical with the first axis of a principle component analysis of resource economic
218 strategy formed by SLA (Cerabolini et al., 2010; Kleyer et al., 2008; Wright et al., 2004), leaf dry matter
219 content (Cerabolini et al., 2010; Kleyer et al., 2008) and leaf N (Fitter & Peat, 1994; Cerabolini et al.,
220 2010; Kleyer et al., 2008; Wright et al., 2004). The bud bank was considered absent (value = 0) when
221 species had fewer than 10 buds between 0 and 10 cm belowground and present (value = 1) when
222 species had more than 10 buds between 0 and 10 cm belowground. Lateral spread was recorded as
223 absent (value = 0), when species did not possess clonal organs for horizontal growth of at least 0.25
224 m y^{-1} and present (value = 1), when species possessed clonal organs for horizontal growth of at least
225 0.25 m y^{-1} .

226 For all three traits, we calculated community-weighted means (CWM) according to the cover of each
227 species, using the vegetation records of the control plots in 2015, i.e. in the first season. Further, we
228 used the same data to calculate functional richness with the package FD version 1.0-12 (Laliberté &
229 Legendre, 2010), without accounting for the abundance of the individual species.

230 Further, we included the seed bank in addition to the functional traits. In October 2014 we took five
231 soil samples of a depth of 10-15 cm in all treatment and control plots, resulting in 10 samples per
232 grassland site and later on observed germination of seeds in the soil bank at the Botanical Garden of
233 the University of Bern, Switzerland. More information on the methodology are in the supplementary
234 material S1.

235 *Statistical analysis*

236 Firstly, we tested the effect of region and disturbance on above- and belowground plant biomass,
237 plant cover, plant species richness and the availability of NO₃-N, NH₄-N, K and PO₄-P using linear mixed
238 models with site as a random factor (package lme4: Bates, Mächler, Bolker, & Walker, 2015). For plant
239 biomass we also included the day of the year of biomass collection as explanatory variable. Variables
240 were transformed (either log- or square-root-transformation) if necessary to achieve normal
241 distribution of their residuals.

242 Secondly, we calculated log-response ratios, hereafter called relative recovery respectively relative
243 nutrient release or lnRR, by taking the logarithm of the non-transformed response variables of the
244 disturbance plot divided by the response variables of the control plot. A lnRR of zero means complete
245 recovery of plant communities and nutrient release after the disturbance, whereas a negative lnRR
246 indicates incomplete recovery of plant communities or a decreased nutrient release. Finally, a positive
247 lnRR indicates increased ecosystem function of plant communities or increased release of nutrients
248 after the disturbance. We also calculated the difference (treatment – control) as absolute recovery
249 and absolute nutrient release, to test whether results differ when absolute rather than relative values

250 are considered, as most studies focus on relative recovery only, which might lead us to overlook
251 biologically important results of applied interest caused by initial differences of the studied systems.

252 Thirdly, we calculated linear models including LUI, resident species richness, soil water content, the
253 three CWM functional traits and number of seedlings from the seed bank as explanatory variables to
254 assess the importance of these variables for relative and absolute recovery of plant communities and
255 nutrient release. To account for regional effects and environmental co-variates that varied within
256 region, for each variable we calculated a linear model including the three regions, soil pH, topographic
257 wetness index (TWI; Sørensen, Zinko, & Seibert, 2006) and soil depth of the grasslands and used the
258 standardized residuals of these models for analyses. Further, we calculated the same linear models
259 using functional richness instead of CWM functional traits and number of seedlings from the seed
260 bank (Table S2) to decide which variables should be included in the fourth step, the structural equation
261 models (SEMs), depending on their importance.

262 Fourthly, we used SEMs to analyse the direct and indirect effects of resident species richness and LUI
263 on the relative and absolute recovery of plant communities and nutrient release, respectively (Fig. S1).
264 In the SEMs, LUI and plant species richness were directly linked to absolute and relative recovery to
265 test their direct effects (Fig. S1). LUI was linked additionally to resident species richness to analyse
266 whether LUI also indirectly affected recovery via resident species richness. We hypothesized that part
267 of the effect of LUI and resident species richness on recovery is mediated by functional composition
268 and recolonization from the seed bank. However, the linear models showed that neither CWM
269 functional traits nor number of seedlings from the seed bank strongly and consistently influenced
270 absolute or relative recovery (Table S2). Therefore, we decided to test the indirect effect of LUI and
271 resident species richness on recovery via functional composition by using functional richness only.
272 With the reduced plant cover after the disturbance, we expected soil water content to potentially
273 influencing recovery. We therefore included soil water content as an additional environmental

274 variable, which correlated with LUI and directly influenced recovery. We calculated separate models
275 for 2015 and 2016 and the absolute and relative recovery of plant communities and nutrient release.
276 Running our SEMs for both, absolute and relative recovery, and separately for the years 2015 and
277 2016 resulted in a total of 24 models. We also tested a SEM with a correlation between resident
278 species richness and CWMs, rather than a directional path from resident species richness to the
279 CWMs. Although the significance of some effects changed in these SEMs, the overall pattern remained
280 the same as in the models presented in the results.

281 **Results**

282 *Effects of disturbance on plant communities and nutrient release*

283 After the disturbance, regrowth of plants occurred from seed germination and resprouting of plant
284 roots and fragments. Despite some newly emerging plant species, most of the species found in the
285 disturbed plots were also present in the control plots (Fig. S2).

286 In the first season, approximately half a year after the experimental sward disturbance, across all
287 grassland sites species richness was increased by 11 % (Fig. 1a), while plant cover (-44 %, Fig. 1b),
288 aboveground biomass (-54 %, Fig. 1c) and belowground biomass (-64 %, Fig. 1d) were decreased. NO_3^-
289 N in soil was increased by 140 % (Fig. 2a), while $\text{NH}_4\text{-N}$ (-39 %, Fig. 2b), K (-35 %, Fig. 2c) and $\text{PO}_4\text{-P}$ (-
290 38 %, Fig. 2d) were reduced. This means that sward disturbance considerably affected all response
291 variables in the first season.

292 In the second season after the disturbance, approximately one and a half year after the experimental
293 sward disturbance, we found that across all grassland sites species richness was still increased by 12
294 % (Fig. 1e) while plant cover (Fig. 1f) and aboveground biomass (Fig. 1g) were not affected by
295 disturbance any longer. Soil nutrient concentrations and belowground biomass were not measured in
296 the second season.

297 We found some regional differences of the treatment effects (Table S1; Fig. S3). While aboveground
298 biomass (Fig. S3a), plant cover (Fig. S3b), plant species richness (Fig. S3c) and release of $\text{NO}_3\text{-N}$ of the
299 first season (Fig. S3d) and aboveground biomass (Fig. S3e) and plant species richness of the second
300 season (Fig. S3g) reacted in the same direction in all regions, but in varying strength, the overall
301 disappearance of the effect of disturbance on plant cover in the second season was mostly due to
302 opposing effects in different regions (Fig. S3f). In the second season after the disturbance, plant cover
303 was still reduced in the disturbance plots in the Schwäbische Alb and Hainich-Dün, but increased in
304 Schorfheide-Chorin (Fig. S3f).

305 *Recovery as affected by functional composition*

306 Testing the importance of the community-weighted mean (CWM) traits specific leaf area, lateral
307 spread and bud bank as well as the number of seedlings from the seed bank for recovery of plant
308 communities and nutrient release showed that none of them had strong effects (Table S2) and their
309 significances and strength was comparable with those of functional richness (Table S2). Therefore, we
310 only included functional richness in the structural equation models (SEMs) reported hereafter.

311 Relative recovery of plant cover (Fig. 3b), above- (Fig. 3c) and belowground biomass (Fig. 3d;
312 marginally significant) but also relative release of $\text{NO}_3\text{-N}$ (Fig. 5a) and $\text{NH}_4\text{-N}$ (Fig. 5b) were increased
313 in grasslands with high functional richness in the first season after the disturbance. In the second
314 season after the disturbance, grasslands with high functional richness had decreased relative recovery
315 of plant cover (Fig. 3f).

316 Absolute recovery of above- (Fig. 4c) and belowground biomass (Fig. 4d) was higher in grasslands with
317 high functional richness than in grasslands with low functional richness in the first season after the
318 disturbance.

319 Overall, grasslands of high functional richness had increased relative and, partly, absolute recovery of
320 plant communities (Table S3) but also increased relative nutrient release (Table S4) after the

321 disturbance than grasslands of low functional richness. The functional richness of grasslands did not
322 matter for relative or absolute recovery of plant communities in the second season (Table S3) and for
323 absolute release of nutrients (Table S4) after the disturbance.

324 *Recovery as affected by resident species richness*

325 When using SEMs to distinguish direct and indirect effects of resident species richness on recovery of
326 plant communities and release of nutrients after sward disturbance, we found that relative recovery
327 of plant species richness (Fig. 3a), plant cover (Fig. 3b; marginally significant), above- (Fig. 3c) and
328 belowground biomass (Fig. 3d; marginally significant) were lower in grasslands of high resident species
329 richness than in grasslands of low resident species richness. This was still the case for the relative
330 recovery of species richness (Fig. 3e) and plant cover (Fig. 3f) in the second season after the
331 disturbance. Further, resident species richness indirectly increased the relative recovery of plant cover
332 (Fig. 3b), above- (Fig. 3c) and belowground biomass (Fig. 3d) in the first season after the disturbance
333 by increasing the functional richness in the respective grassland communities. For relative nutrient
334 release, resident species richness only played a minor role compared with its role for the relative
335 recovery of plant communities (Fig. 5a-d). Grasslands of high resident species richness had lower
336 release of $\text{PO}_4\text{-P}$ than grasslands of low resident species richness (Fig. 5d), while high resident species
337 richness indirectly increased the release of $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ via increasing functional richness (Figs.
338 5a and 5b).

339 Absolute recovery of plant communities was influenced much less by the resident species richness of
340 grassland than relative recovery of plant communities. For the first season after the disturbance, only
341 the indirect positive effect of resident species richness on absolute recovery of above- (Fig. 4c) and
342 belowground biomass (Fig. 4d) via increasing functional richness was significant. In the second season
343 after the disturbance, grasslands of high resident species richness had lower absolute recovery of
344 plant cover (Fig. 4f) and aboveground biomass (Fig. 4g; marginally significant) than grasslands of low
345 resident species richness. For absolute nutrient release, resident species richness also only played a

346 minor role (Figs. 5e-5h). Grasslands of high resident species richness merely had lower absolute
347 release of $\text{NO}_3\text{-N}$ than grasslands of low resident species richness (Fig. 5e).

348 Overall, high resident species richness strongly decreased relative recovery of plant communities
349 (Table S3), while it only played a minor role for the absolute recovery of plant communities (Table S3)
350 and relative and absolute nutrient release (Table S4).

351 *Recovery as affected by land-use intensity*

352 Using SEMs to distinguish direct and indirect effects of LUI, we found that LUI directly affected relative
353 recovery of plant cover in the second season only (Fig. 1f), where high-intensity grasslands had lower
354 recovery of plant cover than low-intensity grasslands. However, high LUI also lead to plant
355 communities with lower resident species richness. Therefore, high LUI indirectly increased the relative
356 recovery of plant communities by decreasing negative effects of resident species richness (Fig. 3).
357 Relative nutrient release was decreased for $\text{NO}_3\text{-N}$ and increased for $\text{NH}_4\text{-N}$ in high-intensity grasslands
358 compared with low-intensity grasslands (Figs. 5a and 5b).

359 Absolute recovery of plant communities was influenced more directly by LUI than relative recovery.
360 Compared with low intensity-grasslands, grasslands under high LUI had increased absolute recovery
361 of species richness (Fig. 4a) and decreased absolute recovery of aboveground biomass (Fig. 4c) in the
362 first season after the disturbance and decreased absolute recovery of plant cover (Fig. 4f) and
363 aboveground biomass (Fig. 4g) in the second season after the disturbance. LUI also indirectly increased
364 absolute recovery of plant cover (Fig. 4f) and aboveground biomass (Fig. 4g) in the second season via
365 decreasing negative direct effects of resident species richness. Absolute nutrient release of $\text{PO}_4\text{-P}$ was
366 the only measured nutrient that was directly affected by LUI, where high-intensity grasslands had
367 lower release of $\text{PO}_4\text{-P}$ than low-intensity grasslands (Fig. 5h). High-intensity grasslands also had
368 increased absolute release of $\text{NO}_3\text{-N}$ due to an indirect effect via decreased resident plant species
369 richness (Fig. 5e).

370 Overall, high LUI frequently increased relative recovery of plant communities indirectly via decreasing
371 resident species richness, but directly decreased absolute recovery of some aspects of plant
372 communities (Tables S3). In addition, LUI had only minor effects on relative and absolute nutrient
373 release (Table S4).

374 **Discussion**

375 *Effects of disturbance on plant communities and nutrient release*

376 In the first season, the effect of experimental sward disturbance on plant communities (Fig. 1) and
377 nutrient release (Fig. 2) was very strong on all 73 grassland sites. While disturbance drastically reduced
378 above- and belowground biomass and plant cover in the first season, it increased plant species
379 richness. This increase in species richness was found in grasslands with low resident species richness,
380 which are managed more intensively and therefore not comparable with the natural, high diversity
381 communities studied by Hirst, Pywell, Marrs, and Putwain (2003) and Biswas and Mallik (2010).
382 Grasslands of high resident species richness, which are managed at low intensity, experienced a
383 decrease in species richness and are therefore comparable with the communities studied by Hirst et
384 al. (2003) and Biswas and Mallik (2010). The increase of species richness in grasslands managed at
385 high intensity was most likely due to reduced plant cover and therefore reduced light competition
386 after the disturbance. This allowed “new” species to establish from the seed bank or seed rain (see
387 also Klaus et al., 2017; Klaus et al., 2018a). Including a wide gradient of resident species richness
388 among our studied grasslands (12 to 70 species on a 4 m x 4 m plot; Fig. S4) enabled us to show that
389 the effect of a disturbance depended on the initial state of the grasslands.

390 After the first season, disturbance effects disappeared for aboveground biomass and plant cover and,
391 on some sites, values from disturbed plots even exceeded those of the control plots, probably due to
392 compensatory growth stimulated by disturbance-related release of nutrients (especially NO₃-N, see
393 below; McNaughton, Wallace, & Coughenour, 1983; Klaus et al., 2018b).

394 Disturbance affected the release of soil nutrients in the first season after the disturbance in different
395 ways. Nitrate ($\text{NO}_3\text{-N}$) was strongly increased and ammonium ($\text{NH}_4\text{-N}$), mobile potassium (K) and
396 phosphate ($\text{PO}_4\text{-P}$) were decreased. The increase of $\text{NO}_3\text{-N}$ was most likely caused by intensive activity
397 of soil organisms making use of dead plant matter (e.g. plant litter, fine and coarse roots; Six, Conant,
398 Paul, & Paustian, 2002). In addition, mechanical perturbation might have disrupted soil aggregates
399 and released protected organic matter (Cuevas, Mastrantonio, Ojeda, & Jaksic, 2012). This is in line
400 with previous studies showing severe nitrate leaching into ground water as one consequence of
401 mechanical sward disturbance (e.g. Whitmore, Bradbury, & Johnson, 1992). The decreased release of
402 $\text{NH}_4\text{-N}$ was presumably due to immediate nitrification caused by increased air volume in the disturbed
403 soil or due to fast processing of ammonia by ammonia oxidizing microorganisms (Jha, Kashyap, &
404 Singh, 1996). The decreased release of K and $\text{PO}_4\text{-P}$ concentrations might have been caused by an
405 increased uptake of these elements by soil microorganisms (living in the topsoil above the resin bags)
406 either due to increased microbial abundance (Lamb, Kennedy, & Siciliano, 2011) and/or changes in
407 microbial community structure (Hendrix et al., 1986). These mechanisms could have been driven by
408 the simultaneous increase in available $\text{NO}_3\text{-N}$ and easily available labile organic matter. Combined with
409 a reduced mobilisation of especially P due to reduced plant activity (e.g. root exudation), this may
410 explain the observed findings.

411 *Relative importance of functional community composition, resident species richness and land-use*
412 *intensity for recovery*

413 In structural equation models (SEMs) resident species richness, land-use intensity or soil water content
414 overall were not strongly related to the recovery of plant communities or nutrient release. The
415 maximum R^2 of 0.24 was found for the absolute recovery of plant cover in the second season after the
416 disturbance (Figs 3-5).

417 Functional composition

418 Overall, the different plant traits characterising mean functional community composition hardly
419 explained the recovery of ecosystem functions. The low importance of specific functional traits for the
420 recovery of ecosystem functions is in contrast with previous studies where community-weighted-
421 mean (CWM) traits were found to explain variation in ecosystem functions (Allan et al., 2015; SLA),
422 stability of communities (Fischer et al., 2016; PCA including several traits) or stability of populations
423 (Májeková, Bello, Doležal, & Lepš, 2014; LDMC, rooting depth, and leaf $\delta^{13}C$; Busch et al., 2018; PCA
424 including several traits). While some of these differences could be due to the consideration of different
425 CWM traits or stability measures, there is also an alternative explanation. Our wide gradient in land-
426 use intensity may have masked effects of CWM traits, such that for instance grasslands with high CWM
427 SLA recovered better if they experienced high land-use intensity, but recovered less well if they
428 experienced low land-use intensity. Thus, we suggest that in agricultural grassland communities,
429 where the diversity and functional composition of communities are strongly influenced by
430 management, effects of CWM traits might be overridden (Grace et al., 2007).

431 Functional richness increased the recovery of several ecosystem functions in the first season after the
432 disturbance, which is in line with previous studies (Diaz & Cabido, 2001; Weigelt, Schumacher, Roscher
433 & Schmid, 2008; Laliberté et al., 2010; Mori, Furukawa & Sasaki, 2012). Complementarity of plant
434 species with different functional traits within a community can increase the chances of having species
435 capable of coping with changed biotic and abiotic conditions after a disturbance, leading to a better
436 recovery of ecosystem functions (insurance hypothesis; Yachi & Loreau, 1999). Next to increasing
437 recovery of plant communities, higher functional richness also increased the relative release of NO_3^- -
438 N and NH_4^+ -N in the disturbed plots compared to the controls most likely due to the loss of plant species
439 with diverse N acquisition strategies. Furthermore, functionally rich plant communities (including
440 leguminous herbs) (Hooper & Vitousek, 1998; Scherer-Lorenzen, Palmberg, Prinz & Schulze, 2003)
441 might favour functional diverse soil microbial communities due to more diverse organic N resources.

442 Altogether, these results suggest that while increasing the CWM of a specific functional trait does not
443 necessarily ensure high stability of ecosystem functions in agricultural grasslands, increasing
444 functional richness has the potential to buffer effects of disturbance on vegetation-related ecosystem
445 functions with the drawback of increased release of nutrients in the soil. To ensure the stability of
446 agricultural grasslands in the light of more frequent and more intensive disturbances, increasing
447 functional richness of the plant community therefore seems to be an important step to take.

448 Resident species richness

449 Grasslands of high resident species richness had lower relative recovery of plant species richness, plant
450 cover, plant biomass (first season only), and PO₄-P than grasslands of low resident species richness.
451 Overall, our findings thus seem to disagree with results from the literature, which often report positive
452 effects of species richness on stability (Frank & McNaughton, 1991; McGrady-Steed, Harris, & Morin,
453 1997; Naeem & Li, 1997; Tilman, Reich, & Knops, 2006). This discrepancy can have several
454 explanations. One difficulty relates to the various definitions and aspects of stability of ecosystems
455 (Grimm & Wissel, 1996). In our study, we considered recovery, i.e. how far ecosystem functions
456 returned to initial conditions. However, other studies reporting positive effects of species richness on
457 stability, considered other stability measures, such as resistance (Frank and McNaughton 1991, Isbell
458 et al., 2015) or variability over time (McGrady-Steed et al., 1997, Naeem & Li, 1997, Tilman et al.,
459 2006). Additionally, there are other studies showing no or negative effects for other stability concepts
460 like resilience, recovery and resistance (Isbell et al., 2015, DeBoeck et al., 2018). Therefore, rather than
461 generally contradicting a positive species richness-stability relationship, we found that grasslands with
462 high species richness suffered more strongly from the disturbance and therefore showed lower
463 relative recovery.

464 A further difference between our study and previous studies is the type and especially the strength of
465 the disturbance considered. Compared with mostly relatively mild climatic disturbances, as
466 considered, for example, by Isbell et al. (2015), our mechanical disturbance was very severe, not only
467 affecting the growth of the plants, but killing plant species and reshaping the entire vegetation. Such

468 a severe disturbance is more similar to the disturbances included in the meta-analysis by DeBoeck et
469 al. (2018). They found, similar to our study, that high species richness does not always buffer the
470 consequences of extreme disturbances. The influence of species richness can depend on the
471 community assembly processes involved, differences in ecosystem sensitivity to disturbances or the
472 specific characteristics of the studied disturbances (DeBoeck et al., 2018).

473 Additionally, comparing results of experimental communities with communities across real-world
474 gradients of diversity is never straightforward (Wardle 2016). Many previous studies analysing species
475 richness-stability relationships manipulated species richness experimentally and often assembled
476 communities from a random pool of species (i.e. Pfisterer & Schmid, 2002; Tilman et al., 2006). Our
477 disturbance experiment was established across a real-world gradient of species richness and therefore
478 community structure was largely the result of land use and abiotic site conditions, which influenced
479 and potentially overrode the effect of functional richness and resident plant species richness for
480 recovery. Our results suggest that under high resident plant species richness the recovery of plant
481 communities can be even decreased after a severe sward disturbance in real-world systems. Overall,
482 our results stress the importance of considering abiotic conditions, the type and strength of a
483 disturbance and the considered stability measure when interpreting the importance of different
484 drivers for stability of plant communities and their ecosystem functions.

485 Land-use intensity

486 In our study, the intensity of grassland management hardly directly affected the relative recovery of
487 plant communities but more often the absolute recovery, especially of aboveground biomass. In the
488 instances when land-use intensity directly affected absolute recovery, high-intensity grasslands had
489 mostly lower recovery. These negative effects can be explained by additional disturbances by grazing
490 and mowing (Vogel et al., 2012; Stampfli et al., 2018) in high-intensity grasslands or by the initially
491 higher aboveground biomass (Socher et al., 2012), which led to a higher absolute loss and therefore
492 reduced absolute recovery of aboveground biomass.

493 Next to these direct negative effects on recovery, high land-use intensity also indirectly increased
494 recovery of plant communities via reducing resident plant species richness. Such indirect effects of
495 land-use intensity via plant species richness have not been studied before but have been shown for
496 the delivery of other ecosystem functions (e.g. Socher et al., 2012; Allan et al., 2015). The indirect
497 positive effect of land-use intensity on recovery via a reduction of resident species richness was
498 probably caused by higher nutrient input on fertilized grasslands, which could be used more efficiently
499 by a lower number of more competitive plant species (Allan et al., 2015).

500 High land-use intensity also had a positive effect, namely on absolute species richness after the
501 disturbance. This can be explained by increased light availability, which promoted weak competitors
502 (Hautier, Niklaus, & Hector, 2009), an effect that was likely to be stronger in grasslands with high land-
503 use intensity where plant biomass was initially high and plant cover dense. Furthermore, simple plant
504 communities consisting of 12 plant species are more likely to regenerate than more complex
505 communities consisting of 60 plant species. We also found that low-intensity grasslands had a larger
506 relative increase of released $\text{NO}_3\text{-N}$ compared with grasslands with high land-use intensity, which was
507 very likely caused by the already high release of $\text{NO}_3\text{-N}$ in grasslands with high land-use intensity even
508 without the presence of a disturbance (Klaus et al., 2018b).

509 Our results show that effects of land-use intensity on the recovery of plant communities across real-
510 world environmental gradients are complex. Differences between direct and indirect effects show the
511 importance of disentangling these effects experimentally or by using specific statistical methods like
512 SEMs.

513 Absolute versus relative recovery

514 The differences between the drivers of absolute versus relative recovery were most pronounced for
515 land-use intensity and resident plant species richness for the recovery of plant cover and aboveground
516 biomass. These two ecosystem functions are the ones that farmers try to maximise in agricultural
517 grasslands, wherefore their initial levels correlate most strongly with land-use intensity. Absolute

518 recovery does not correct for differences in initial conditions, wherefore grasslands with high initial
519 ecosystem functions (i.e. high biomass, high plant cover) showed lower recovery, at least on the short-
520 term. While the relative recovery enabled us to study the effects of our explanatory variables on
521 recovery independent of their initial absolute differences among grasslands and resulted in more
522 mechanistic findings, absolute recovery helped to understand the meaning of a disturbance for the
523 system when starting conditions vary widely and therefore resulted in more applied findings.

524 *Conclusion*

525 We show that disentangling the importance of land-use intensity, resident species richness and
526 functional composition on the recovery of plant communities and nutrient release is important to
527 understand which direct and indirect effects are involved in increasing and decreasing the stability of
528 agricultural grasslands. In a time of increasing intensification of land use, it is important to note, that
529 high land-use intensity can have negative effects on the recovery of some ecosystem functions but
530 also that plant species richness of high-intensity grasslands can increase after sward disturbance, at
531 least temporarily. Still, highly important is that effects of land-use intensity on recovery of ecosystem
532 functions can be influenced by changes in species richness and functional richness. An increase of
533 species richness alone, i.e. without changes in functional richness, might reduce the recovery of some
534 ecosystem functions. However, an increase of functional richness along with an increase of resident
535 species richness could help to buffer effects of severe disturbances on grassland plant communities
536 and their functioning. To increase the capacity for stability of agricultural grasslands, we therefore
537 suggest the enrichment of agricultural grasslands with functionally different plant species.

538 **Acknowledgements**

539 We thank Ulrike Berning-Mader, Melanie Tappe and Lennart Friedritz for help with chemical analyses
540 and Stefan Blaser, Samuel Massa, Armin Komposch, Nico Heer, Svenja Kunze, Martin Freitag, Dirk
541 Trompeter, Ann-Kathrin Will and Melanie Eckert for help during fieldwork.

542 We thank the managers of the three Exploratories, Kirsten Reichel-Jung, Katrin Lorenzen, and Martin
543 Gorke and all former managers for the project infrastructure; Christiane Fischer and Simone Pfeiffer
544 for giving support through the central office, Michael Owonibi for managing the central data base, and
545 Eduard Linsenmair, Dominik Hessenmöller, Ingo Schöning, François Buscot, Ernst-Detlef Schulze,
546 Wolfgang W. Weisser and the late Elisabeth Kalko for their role in setting up the Biodiversity
547 Exploratories program.

548 The work has been funded by the DFG Priority Program 1374 "Infrastructure-Biodiversity-
549 Exploratories" (HO 3830/2-3; FI 1246/15-2; PR 728/2-3). Fieldwork permits were issued by the
550 responsible state environmental offices of Baden-Württemberg, Thüringen, and Brandenburg
551 (according to § 72 BbgNatSchG). This study has also been supported by the TRY initiative on plant
552 traits (<http://www.try-db.org>), hosted, developed and maintained by J. Kattge and G. Bönisch (Max
553 Plank Institute for Biogeochemistry, Jena, Germany). TRY is currently supported by DIVERSITAS/Future
554 Earth and the German Centre for Integrative Biodiversity Research (iDiv) Halle---Jena---Leipzig.

555 **Authors' contribution**

556 DP, NH and MF conceived and designed the experiment. DS, VHK, TK, IS, SW, RSB, SM, EK, JH, SN and
557 UH collected and contributed the data. DS, VHK, NH, MF and DP analysed the data and drafted the
558 manuscript. All authors contributed to revise the manuscript and gave final approval for publication.

559 **Data accessibility**

560 Data is stored in the BExIS database of the Biodiversity Exploratories program and can be accessed
561 upon request.

562 **References**

- 563 Allan, E., Manning, P., Alt, F., Binkenstein, J., Blaser, S., & Blüthgen, N., ... Fischer, M. (2015). Land use
564 intensification alters ecosystem multifunctionality via loss of biodiversity and changes to functional
565 composition. *Ecology letters*, 18(8), 834–843. doi: 10.1111/ele.12469.
- 566 Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4.
567 *Journal of Statistical Software*, 67(1). doi: 10.18637/jss.v067.i01.
- 568 Biswas, S.R. & Mallik, A.U. (2010). Disturbance effects on species diversity and functional diversity in
569 riparian and upland plant communities. *Ecology*, 91(1), 28–35. doi: 10.1890/08-0887.1.
- 570 Blüthgen, N., Dormann, C.F., Prati, D., Klaus, V.H., Kleinebecker, T., & Hölzel, N., ... Weisser, W.W.
571 (2012). A quantitative index of land-use intensity in grasslands: Integrating mowing, grazing and
572 fertilization. *Basic and Applied Ecology*, 13(3), 207–220. doi: 10.1016/j.baae.2012.04.001.
- 573 Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., & Boch, S., ... Gossner, M.M. (2016). Land
574 use imperils plant and animal community stability through changes in asynchrony rather than
575 diversity. *Nature communications*, 7, 10697. doi: 10.1038/ncomms10697.
- 576 Busch, V., Klaus, V.H., Penone, C., Schäfer, D., Boch, S., & Prati, D., ... Kleinebecker, T. (2018). Nutrient
577 stoichiometry and land use rather than species richness determine plant functional diversity. *Ecology*
578 *and Evolution*, 8(1), 601–616. doi: 10.1002/ece3.3609.
- 579 Cerabolini, B.E.L., Brusa, G., Ceriani, R.M., Andreis, R. de, Luzzaro, A., & Pierce, S. (2010). Can CSR
580 classification be generally applied outside Britain? *Plant Ecology*, 210(2), 253–261. doi:
581 10.1007/s11258-010-9753-6.
- 582 Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., & Gurvich, D.E., ... Poorter, H. (2003).
583 A handbook of protocols for standardised and easy measurement of plant functional traits worldwide.
584 *Australian Journal of Botany*, 51(4), 335–380. doi: 10.1071/BT02124.

585 Cuevas, M.F., Mastrantonio, L., Ojeda, R.A., & Jaksic, F.M. (2012). Effects of wild boar disturbance on
586 vegetation and soil properties in the Monte Desert, Argentina. *Mammalian Biology - Zeitschrift für*
587 *Säugetierkunde*, 77(4), 299–306. doi: 10.1016/j.mambio.2012.02.003.

588 DeBoeck, H.J., Bloor, J.M.G., Kreyling, J., Ransijn, J.C.G., Nijs, I., Jentsch, A., & Zeiter, M. (2018). Patterns
589 and drivers of biodiversity-stability relationships under climate extremes. *Journal of Ecology*, 106(3),
590 890-902. doi: 10.1111/1365-2745.12897.

591 Dornelas, M. (2010). Disturbance and change in biodiversity. *Philosophical Transactions B*, 365(1558),
592 3719-3727. doi: 10.1098/rstb.2010.0295

593 European Communities (2008). LIFE and Europe's grasslands. Restoring a forgotten habitat: Office for
594 Official Publications of the European Communities, Luxembourg. doi: 10.2779/23028

595 Fischer, F.M., Wright, A.J., Eisenhauer, N., Ebeling, A., Roscher, C., & Wagg, C., ... Pillar, V.D. (2016).
596 Plant species richness and functional traits affect community stability after a flood event. *Philosophical*
597 *transactions of the Royal Society of London. Series B, Biological sciences*, 371(1694). doi:
598 10.1098/rstb.2015.0276.

599 Fischer, M., Bossdorf, O., Gockel, S., Hänsel, F., Hemp, A., & Hessenmöller, D., ... Weisser, W.W. (2010).
600 Implementing large-scale and long-term functional biodiversity research: The Biodiversity
601 Exploratories. *Basic and Applied Ecology*, 11(6), 473–485. doi: 10.1016/j.baae.2010.07.009.

602 Fitter, A.H. & Peat, H.J. (1994). The ecological flora database. *Journal of Ecology*, 82(2), 415-425. doi:
603 10.2307/2261309.

604 Frank, D.A. & McNaughton, S.J. (1991). Stability increases with diversity in plant communities:
605 Empirical evidence from the 1988 Yellowstone drought. *Oikos*, 62(3), 360-362. doi: 10.2307/3545501.

606 Grace, J.B., Anderson, M.T., Smith, M.D., Seabloom, E., Andelman, S.J., & Meche, G., ... Willig, M.R.
607 (2007). Does species diversity limit productivity in natural grassland communities? *Ecology letters*,
608 10(8), 680–689. doi: 10.1111/j.1461-0248.2007.01058.x.

609 Grman, E., Lau, J.A., Schoolmaster, D.R., & Gross, K.L. (2010). Mechanisms contributing to stability in
610 ecosystem function depend on the environmental context. *Ecology letters*, 13(11), 1400–1410. doi:
611 10.1111/j.1461-0248.2010.01533.x.

612 Hallett, L.M., Stein, C., & Suding, K.N. (2017). Functional diversity increases ecological stability in a
613 grazed grassland. *Oecologia*, 183(3), 831–840. doi: 10.1007/s00442-016-3802-3.

614 Hautier, Y., Niklaus, P.A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after
615 eutrophication. *Science*, 324(5927), 636–638. doi: 10.1126/science.1169640.

616 Hautier, Y., Seabloom, E.W., Borer, E.T., Adler, P.B., Harpole, W.S., & Hillebrand, H., ... Hector, A.
617 (2014). Eutrophication weakens stabilizing effects of diversity in natural grasslands. *Nature*,
618 508(7497), 521–525. doi: 10.1038/nature13014.

619 Hendrix, P.F., Parmelee, R.W., Crossley, D.A., Coleman, D.C., Odum, E.P., & Groffman, P.M. (1986).
620 Detritus food Webs in conventional and no-tillage agroecosystems. *BioScience*, 36(6), 374–380. doi:
621 10.2307/1310259.

622 Hirst, R.A., Pywell, R.F., Marrs, R.H., & Putwain, P.D. (2003). The resistance of a chalk grassland to
623 disturbance. *Journal of Applied Ecology*, 40(2), 368–379. doi: 10.1046/j.1365-2664.2003.00800.x.

624 Hooper, D., Vitousek, P.M. (1998). Effects of plant composition and diversity on nutrient cycling.
625 *Ecological Monographs*, 68(1), 121-149. doi: 10.2307/2657146

626 Jha, P.B., Kashyap, A.K., & Singh, J.S. (1996). Effect of fertilizer and organic matter inputs on nitrifier
627 populations and N-mineralization rates in a dry tropical region, India. *Applied Soil Ecology*, 4(3), 231–
628 241. doi: 10.1016/S0929-1393(96)00110-2.

629 Kayler, E.Z., DeBoeck, H.J., Fatichi, S., Grünzweig, J.M., Merbold, L., Beier, C., ... , Dukes, J.S. (2015).
630 Experiments to confront the environmental extremes of climate change. *Frontiers in Ecology and the*
631 *Environment*, 13(4), 219-225. doi: 10.1890/140174.

632 Kattge, J., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., & Bönisch, G., ... Wirth, C. (2011). TRY - a global
633 database of plant traits. *Global Change Biology*, 17(9), 2905–2935. doi: 10.1111/j.1365-
634 2486.2011.02451.x.

635 Klaus, V.H., Hoever, C.J., Fischer, M., Hamer, U., Kleinebecker, T., & Mertens, D., ... Hölzel, N. (2018a).
636 Contribution of the soil seed bank to the restoration of temperate grasslands by mechanical sward
637 disturbance. *Restoration Ecology*, 26, 114-122. doi:10.1111/rec.12626.

638 Klaus, V.H., Kleinebecker, T., Busch, V., Fischer, M., Hölzel, N., & Nowak, S., ... Hamer, U. (2018b). Land-
639 use intensity, rather than plant species richness, affects the leaching risk of multiple nutrients from
640 permanent grasslands. *Global Change Biology*, 24, 2828-2840. doi:10.1111/gcb.14123

641 Klaus, V.H., Schäfer, D., Kleinebecker, T., Fischer, M., Prati, D., & Hölzel, N. (2017). Enriching plant
642 diversity in grasslands by large-scale experimental sward disturbance and seed addition along
643 gradients of land-use intensity. *Journal of Plant Ecology*, 10(4), 581-591. doi: 10.1093/jpe/rtw062.

644 Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., & Sonnenschein, M., ... Peco, B.
645 (2008). The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *Journal*
646 *of Ecology*, 96(6), 1266–1274. doi: 10.1111/j.1365-2745.2008.01430.x.

647 Klimešová, J. & de Bello, F. (2009). CLO-PLA: The database of clonal and bud bank traits of Central
648 European flora. *Journal of Vegetation Science*, 20(3), 511–516. doi: 10.1111/j.1654-
649 1103.2009.01050.x.

650 Laliberté, E. & Legendre, P. (2010). A distance-based framework for measuring functional diversity
651 from multiple traits. *Ecological Society of America*, 91(1), 299-305. doi: 10.1890/08-2244.1.

652 Laliberté, E., Wells, J.A., Declerck, F., Metcalfe, D.J., Catterall, C.P. & Queiroz, C., ... Mayfield, M.M.
653 (2010). Land-use intensification reduces functional redundancy and response diversity in plant
654 communities. *Ecology Letters*, 13, 76–86.

655 Lamb, E.G., Kennedy, N., & Siciliano, S.D. (2011). Effects of plant species richness and evenness on soil
656 microbial community diversity and function. *Plant and Soil*, 338(1-2), 483–495. doi: 10.1007/s11104-
657 010-0560-6.

658 Májeková, M., de Bello, F., Doležal, J., & Lepš, J. (2014). Plant functional traits as determinants of
659 population stability. *Ecology*, 95(9), 2369–2374. doi: 10.1890/13-1880.1.

660 Massei, G. & Genov, P.V. (2004). The environmental impact of wild boar. *Galemys*, 16, 135–145.

661 McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405(6783), 228–233. doi:
662 10.1038/35012234.

663 McGrady-Steed, J., Harris, P.M., & Morin, P.J. (1997). Biodiversity regulates ecosystem predictability.
664 *Nature*, 390(6656), 162–165. doi: 10.1038/36561.

665 McNaughton, S.J., Wallace, L.L., & Coughenour, M.B. (1983). Plant Adaptation in an Ecosystem
666 Context: Effects of defoliation, nitrogen, and water on growth of an african C4 sedge. *Ecology*, 64(2),
667 307–318. doi: 10.2307/1937078.

668 Naeem, S. & Li, S. (1997). Biodiversity enhances ecosystem reliability. *Nature*, 390(6659), 507–509.
669 doi: 10.1038/37348.

670 Pfestorf, H., Weiß, L., Müller, J., Boch, S., Socher, S.A., & Prati, D., ... Jeltsch, F. (2013). Community
671 mean traits as additional indicators to monitor effects of land-use intensity on grassland plant
672 diversity. *Perspectives in Plant Ecology, Evolution and Systematics*, 15(1), 1–11. doi:
673 10.1016/j.ppees.2012.10.003.

674 Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease the stability of
675 ecosystem functioning. *Nature*, 416(6876), 84–86. doi: 10.1038/416084a.

676 Scherer-Lorenzen, M., Palmberg, C., Prinz, A., Schulze, D.-E. (2003). The role of plant diversity and
677 composition for nitrate leaching in grasslands. *Ecology*, 84(6), 1539-1552. doi: 10.1890/0012-
678 9658(2003)084[1539:TROPDA]2.0.CO;2

679 Sibbesen, E. (1977). A simple ion-exchange resin procedure for extracting plant-available elements
680 from soil. *Plant and Soil*, 46, 665–669. doi: 10.1007/BF00015928

681 Six, J., Conant, R.T., Paul, E.A., & Paustian, K. (2002). Stabilization mechanisms of soil organic matter:
682 Implications for C-saturation of soils. *Plant and Soil*, 241(2), 155–176. doi: 10.1023/A:1016125726789.

683 Skogley, E.O. & Dobermann, A. (1996). Synthetic ion-exchange resins: Soil and environmental studies.
684 *Journal of Environment Quality*, 25(1), 13. doi: 10.2134/jeq1996.00472425002500010004x.

685 Socher, S.A., Prati, D., Boch, S., Müller, J., Klaus, V.H., & Hölzel, N., ... Wilson, S. (2012). Direct and
686 productivity-mediated indirect effects of fertilization, mowing and grazing on grassland species
687 richness. *Journal of Ecology*, 100(6), 1391–1399. doi: 10.1111/j.1365-2745.2012.02020.x.

688 Sørensen, R., Zinko, U., & Seibert, J. (2006). On the calculation of the topographic wetness index:
689 Evaluation of different methods based on field observations. *Hydrology and Earth System Sciences*,
690 10(1), 101–112. doi: 10.5194/hess-10-101-2006.

691 Thompson, K., Bakker, J.P., & Bekker, R.M. (1997). The soil seed banks of north west europe:
692 Methodology, Density and Longevity. Cambridge: Cambridge University Press, 1997. *The New*
693 *phytologist*, 136(2), 369–373. doi: 10.1046/j.1469-8137.1997.00745-2.x.

694 Tilman, D., Reich, P.B., & Knops, J.M.H. (2006). Biodiversity and ecosystem stability in a decade-long
695 grassland experiment. *Nature*, 441(7093), 629–632. doi: 10.1038/nature04742.

696 Weigelt, A., Schumacher, J., Roscher, C., & Schmid, B. (2008). Does biodiversity increase spatial
697 stability in plant community biomass? *Ecology letters*, 11(4), 338–347. doi: 10.1111/j.1461-
698 0248.2007.01145.x.

699 Whitmore, A.P., Bradbury, N.J., & Johnson, P.A. (1992). Potential contribution of ploughed grassland
700 to nitrate leaching. *Agriculture, Ecosystems & Environment*, 39(3-4), 221–233. doi: 10.1016/0167-
701 8809(92)90056-H.

702 Wilson, J.B., Peet, R.K., Dengler, J., Pärtel, M., & Palmer, M. (2012). Plant species richness: The world
703 records. *Journal of Vegetation Science*, 23(4), 796–802. doi: 10.1111/j.1654-1103.2012.01400.x.

704 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., & Bongers, F., ... Villar, R. (2004). The
705 worldwide leaf economics spectrum. *Nature*, 428(6985), 821–827. doi: 10.1038/nature02403.

706 Yachi, S. & Lreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment:
707 The insurance hypothesis. *PNAS*, 96(4), 1463-1468.

708 Yang, H., Jiang, L., Li, L., Li, A., Wu, M., & Wan, S. (2012). Diversity-dependent stability under mowing
709 and nutrient addition: Evidence from a 7-year grassland experiment. *Ecology letters*, 15(6), 619–626.
710 doi: 10.1111/j.1461-0248.2012.01778.x.

Figures and Tables

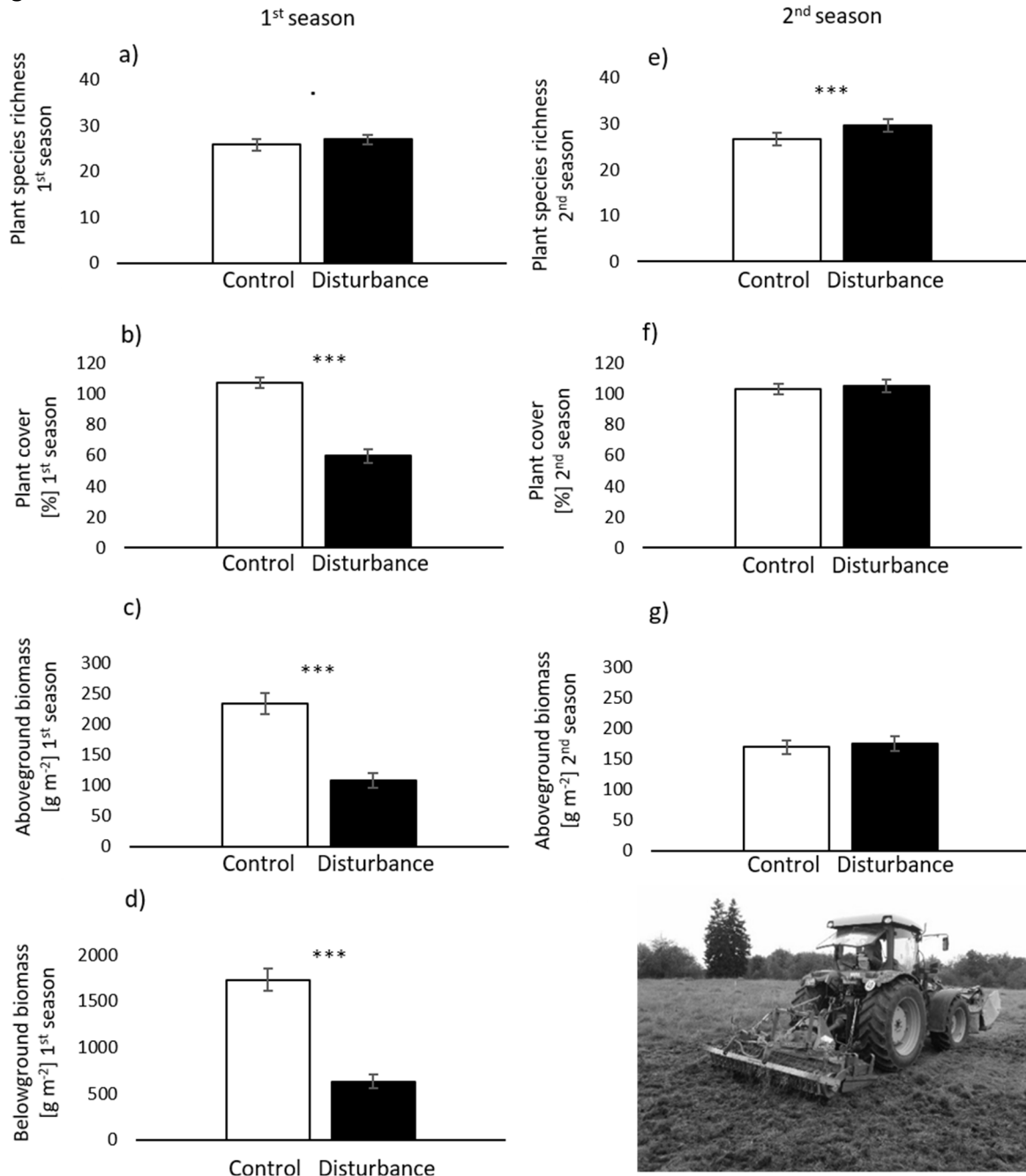


Figure 1: Effects of sward disturbance on plant communities in 73 grasslands differing in land-use intensity. Mean values over all three study regions of (a) plant species richness of the first season, (b) plant cover of the first season, (c) plant aboveground biomass [g m⁻²] of the first season, (d) belowground biomass [g m⁻²] of the first season, (e) plant species richness of the second season, (f) plant cover of the second season, (g) plant aboveground biomass [g m⁻²] of the second season according to the different treatments (control and disturbance) and (h) photograph of the sward disturbance treatment using a rotary harrow (picture VH Klaus)

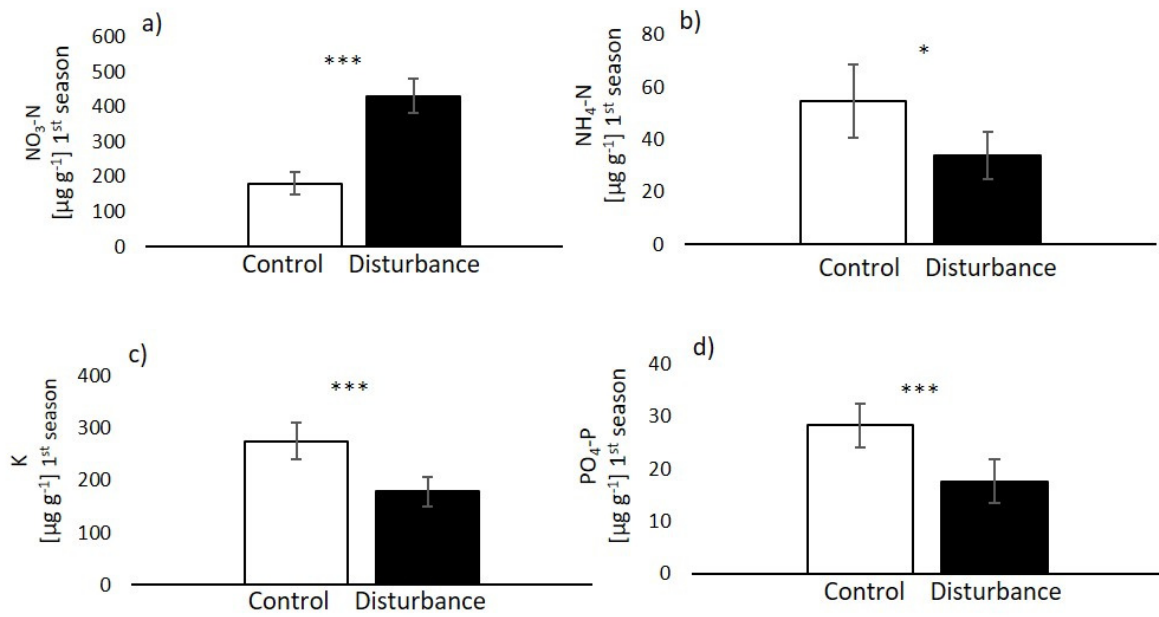


Figure 2: Effects of sward disturbance on nutrient availability in 73 grasslands differing in land-use intensity. Mean values over all three study regions of (a) $\text{NO}_3\text{-N}$, (b) $\text{NH}_4\text{-N}$, (c) K, and (d) $\text{PO}_4\text{-P}$ according to the different treatments.

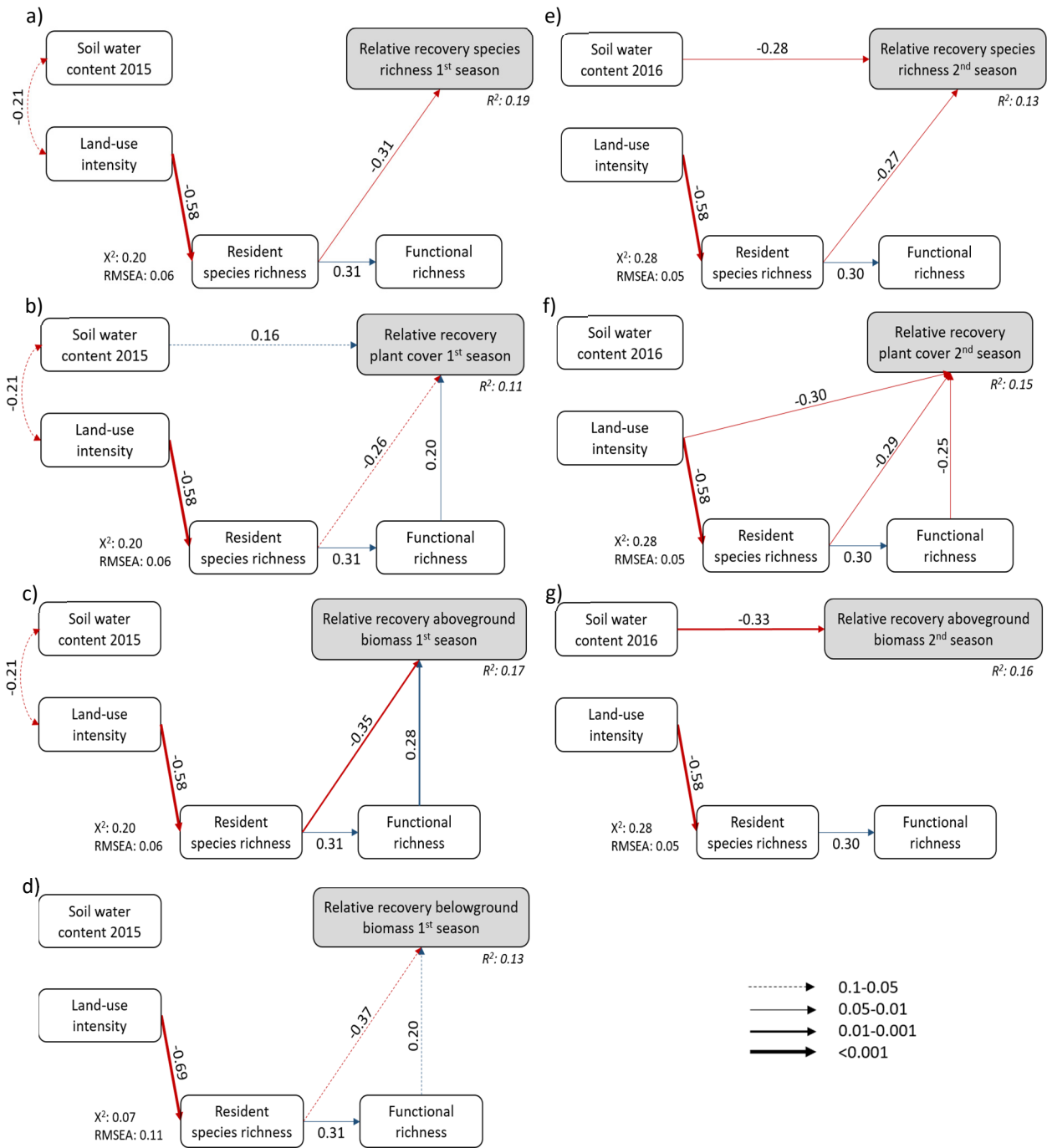
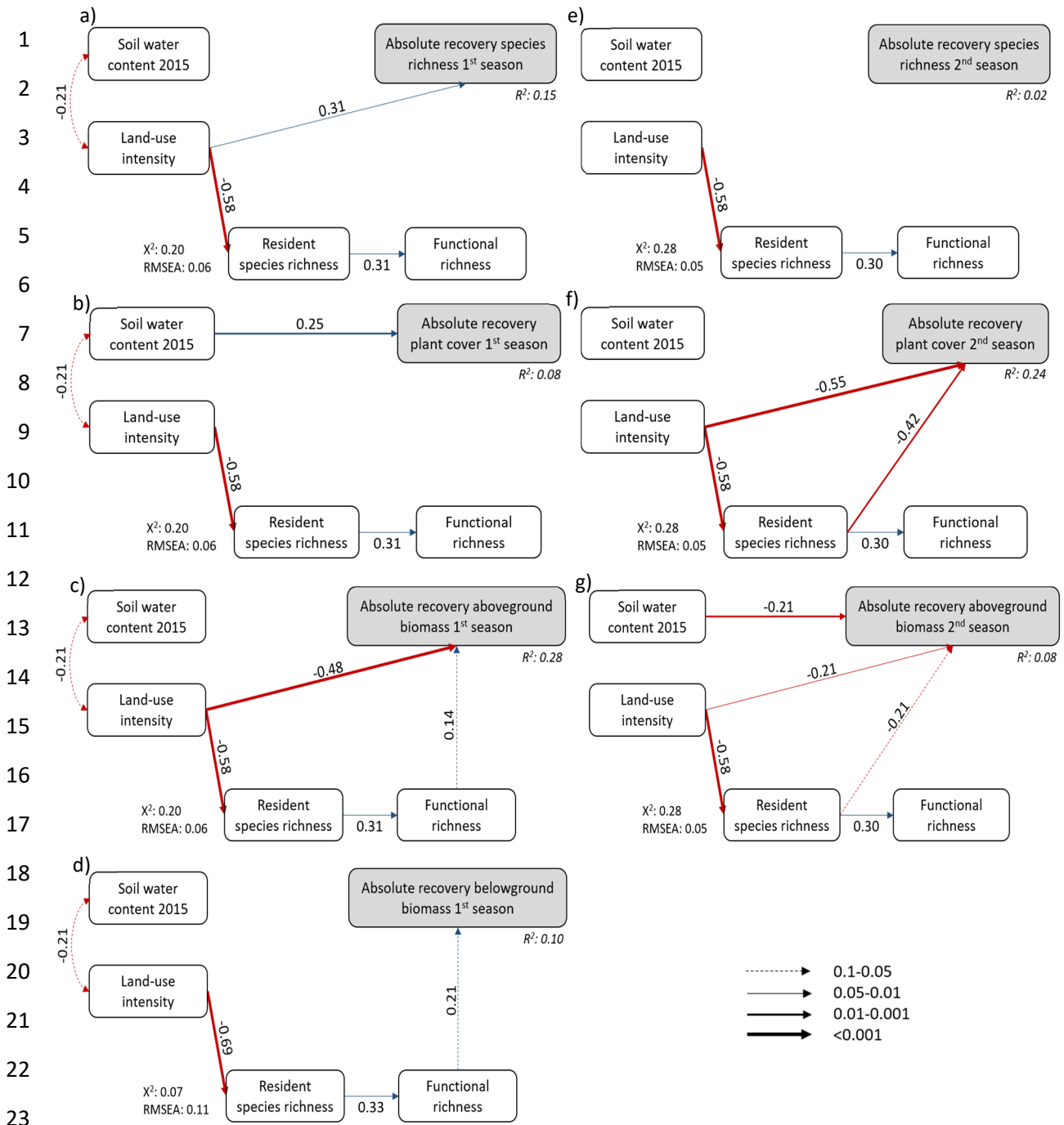
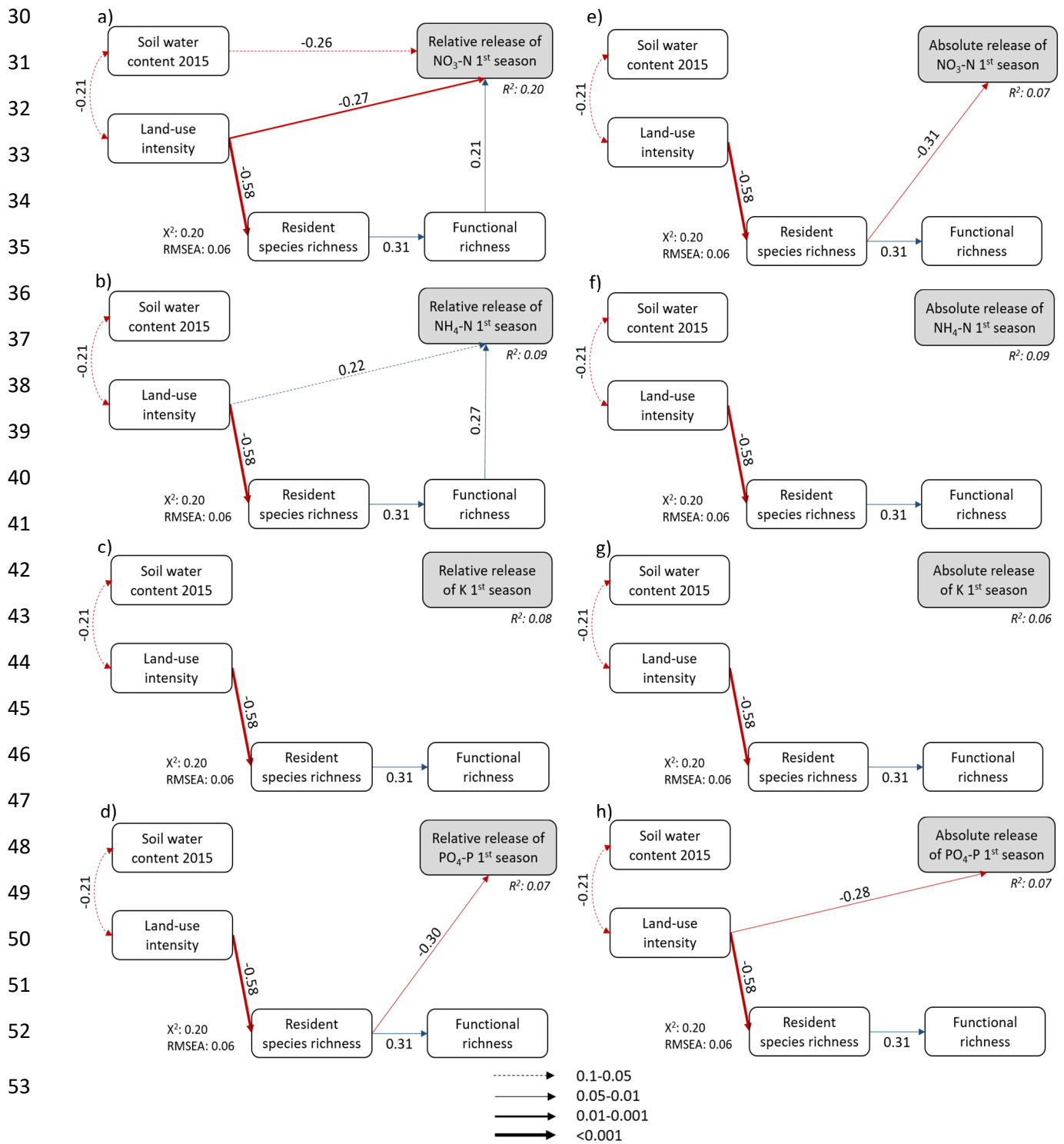


Figure 3: Structural equation models showing direct and indirect effects of different drivers of relative recovery, calculated as $\ln(\text{disturbance}/\text{control})$, for plant species richness and plant related ecosystem functions in the (a-d) first and (e-f) second season after the disturbance. The R^2 of the response variable “relative recovery” is given for each SEM. Further, for each SEM the model fit parameters X^2 ($X^2 > 0.05$ indicates good model fit) and RMSEA (RMSEA < 0.08 indicates good model fit) are given.



24 **Figure 4:** Structural equation models showing direct and indirect effects of different drivers of absolute
 25 recovery, calculated as $\ln(\text{disturbance} - \text{control})$, for plant species richness and plant related
 26 ecosystem functions in the (a-d) first and (e-g) second season after the disturbance. The R² of the
 27 response variable “relative recovery” is given for each SEM. Further, for each SEM the model fit
 28 parameters X² (X² > 0.05 indicates good model fit) and RMSEA (RMSEA < 0.08 indicates good model
 29 fit) are given.



54 **Figure 5:** Structural equation models showing direct and indirect effects of different drivers of (a-d)
 55 relative ($\ln(\text{disturbance}/\text{control})$) and (e-h) absolute ($\text{disturbance} - \text{control}$) recovery of nutrient
 56 release after the disturbance. The R^2 of the response variable “relative recovery” is given for each
 57 SEM. Further, for each SEM the model fit parameters χ^2 ($\chi^2 > 0.05$ indicates good model fit) and RMSEA
 58 (RMSEA < 0.08 indicates good model fit) are given.