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

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Abstract

1. Drivers of ecosystem stability have been a major topic in ecology for decades. Most studies have focused on the influence of species richness on ecosystem stability and found positive diversity-stability relationships. However, land use and abiotic factors shape species richness and functional composition of plant communities and may override species richness-stability relations in managed grasslands.

2. We analysed the relative importance of land-use intensity (LUI), resident plant species richness and functional composition for recovery of plant communities (plant species richness, plant cover, above- and below-ground biomass) and release of soil nutrients after a severe mechanical disturbance. Experimental sward disturbance was applied to 73 grassland sites along a LUI gradient in three German regions. We considered relative (ln(disturbance/control)) and absolute (disturbance – control) treatment effects. Using structural equation modelling, we disentangled direct effects of LUI and resident species richness on recovery and indirect effects via changes in functional richness.

3. Community-weighted-mean traits rarely mattered for recovery or nutrient release, while functional richness especially increased relative recovery of plant communities but also relative release of NO_3-N and NH_4-N. These effects were enhanced by increasing resident plant species richness and decreasing LUI. Next to these indirect influences of LUI and resident plant species richness via functional community composition, grasslands of high compared with grasslands of low resident plant species richness generally showed decreased recovery of plant communities. In grasslands of high LUI, absolute recovery of some aspects of plant

communities was decreased. We did not find consistent differences between the relative importance of the different drivers of recovery after the first and the second season. Overall, resident species richness seemed most important for relative recovery and less important for absolute recovery, where direct effects of LUI were more common.

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

1 | INTRODUCTION

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

Species richness has been frequently suggested to increase stability, as defined by different concepts, including the recovery of ecosystem functions (DeBoeck et al., 2018; Isbell et al., 2015; McCann, 2000). One mechanism leading to increased stability with high species richness is the insurance effect, i.e. the idea that a community with many species is more likely to contain a species with traits adapted to a specific disturbance (Yachi & Loreau, 1999). However, in natural ecosystems, the influence of species richness on the recovery of ecosystem functions could be confounded by environmental gradients, such as land-use intensity. Such confounding effects are rarely studied (Blüthgen et al., 2016; Grman, Lau, Schoolmaster, & Gross, 2010; Hautier et al., 2014; Yang et al., 2012). On one hand, land-use intensity may directly reduce recovery of ecosystem functions, due to additional disturbances from removing biomass via mowing or grazing (Stampfli, Bloor, Fischer, & Zeiter, 2018; Vogel, Scherer-Lorenzen, & Weigelt, 2012) and on the other hand it could directly increase recovery of ecosystem functions by adding nutrients via fertilization, which for example promotes biomass regrowth after a disturbance (Loeser, Sisk, & Crews, 2007). However, high land-use intensity also reduces plant species richness (Allan et al., 2015; Hautier et al., 2014; Socher et al., 2012) and

changes community functional composition and richness, which can have subsequent, indirect effects on recovery (Allan et al., 2015). Decreasing species richness and functional richness could lead to negative indirect effects of high land-use intensity on the recovery of plant communities and their ecosystem functions, as described above. Then again, changes in the functional composition of plant communities, due to high land-use intensity, e.g. an increase in exploitative species with faster regrowth capacity (Allan et al., 2015; Pfestorf et al., 2013), could also lead to indirect positive effects of high land-use intensity on recovery of plant communities and ecosystem functions. Managed grasslands cover vast parts of the earth surface, are amongst the most species rich communities world-wide and provide many different ecosystem services (Allan et al., 2015; Wilson, Peet, Dengler, Pärtel, & Palmer, 2012). To understand the potential for recovery of the functions of this very important ecosystem after a disturbance, it is critical to study land-use intensity, plant species richness and functional community composition together and to disentangle their direct and indirect effects.

Most studies have looked at the effect of relatively weak disturbances like short drought periods (e.g. Frank & McNaughton, 1991) or grazing (e.g. Hallett, Stein, & Suding, 2017), while far fewer have considered recovery after strong disturbances (DeBoeck et al., 2018), such as severe droughts or mechanical disturbances. After a severe disturbance, as occurs in agriculturally used grasslands during grassland renewal (European Communities, 2008) or due to the activity of wild boars (Massei & Genov, 2004), large parts of the plant community are completely disrupted. Here, plant community characteristics, i.e. species richness and functional composition, might be less important for recovery of ecosystem functions than after weak disturbances, and land-use intensity and changes in abiotic conditions such as soil water content could play a more important role. The relative importance of different drivers might therefore be very

different for the recovery after severe disturbances compared with recovery after weak disturbances (DeBoeck et al., 2018; Dornelas, 2010). Therefore, more studies analysing recovery after severe disturbances are needed to understand the role of different drivers under these circumstances.

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

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

1. Grasslands with high functional richness and grasslands with high resident species richness show faster recovery of their functions and lower nutrient release than grasslands with low functional richness and low resident species richness.
2. High land-use intensity directly increases recovery of plant communities and nutrient release but indirectly decreases the recovery of functions and nutrient release via decreasing resident species richness and functional richness.

2 | MATERIALS AND METHODS

2.1 | Study site

Field work took place from 2014 to 2016 on 73 permanent agricultural grassland sites located in three German regions, as part of the large-scale and long-term Biodiversity Exploratories program (Fischer et al., 2010). The three different regions are the Schwäbische Alb (25 sites) in SW-Germany, the Hainich-Dün (23 sites) in Central Germany and the Schorfheide-Chorin (25 sites) in NE-Germany. Details on regional characteristics, including climate and soils, are given in Fischer et al. (2010). The grassland sites were chosen along local land-use intensity gradients, which are

comparable between the different regions (Blüthgen et al., 2012; Fischer et al., 2010) and are typical for grassland management in central Europe. The sites have been used as grasslands for a minimum of 30 years (Fischer et al., 2010).

To determine the land-use intensity we gathered information from farmers with a standardized questionnaire. We inquired about the amount of fertilizer applied (kg nitrogen × ha^{-1} × $year^{-1}$), the frequency of mowing (number of cuts × $year^{-1}$) and the grazing intensity (number of livestock units × grazing days × ha^{-1} × $year^{-1}$). Based on these data we calculated an index of land-use intensity (LUI) according to Blüthgen et al. (2012) by extracting the square root of the sum of fertilization, grazing and mowing intensities for each grassland after dividing each component by its respective mean across all sites, in 2014.

$$LUI = \sqrt{\frac{fertilizer_{site}}{fertilizer_{mean}} + \frac{mowing_{site}}{mowing_{mean}} + \frac{grazing_{site}}{grazing_{mean}}}$$

This resulted in a continuous LUI index, which ranged from 0 to 3.5 (dimensionless). For example, a very low LUI of 0.5 can be achieved through 30 days of grazing by one livestock unit of cattle ha^{-1} $year^{-1}$, an intermediate LUI of 1.5 corresponds to a meadow, which is mown twice and receives 60 kg N ha^{-1} $year^{-1}$ and a relatively high LUI of 3.0 corresponds to a meadow which is mown three times and receives 130 kg N ha^{-1} $year^{-1}$. The grasslands additionally comprise a gradient of plant species richness, which was measured for each grassland independently in close proximity to the treatment plots on 4 m × 4 m plots in May and June 2014 (Socher et al., 2012), hereafter referred to as resident plant species richness. Both LUI and resident plant species richness were used as explanatory variables.

2.2 | Experimental design

We conducted a field experiment on two 7 m × 7 m plots on each of the 73 agricultural grassland sites, consisting of a control and a disturbance plot. The disturbance treatment consisted of an intensive mechanical perturbation of the sward and the upper 10 cm of the soil with a rotary harrow (Schwäbische Alb and Hainich-Dün) or a rotary cultivator (Schorfheide-Chorin) in October 2014 after the regular grassland management practices on the sites had ended for this year. We chose different methods for sward disturbance according to the methods typically used in the respective regions. After disturbance, root and shoot fragments of the plants remained on the plots and the regular management by the farmers continued.

2.3 | Plant species richness and productivity

In May and June 2015 and 2016, we recorded plant species richness on 2 m × 2 m subplots, located in the treatment plots in all grasslands and estimated the cover percentage of each species. For total plant cover, we summed the cover of all species. At the

same time, we assessed productivity as above-ground and below-ground biomass. For above-ground biomass, we cut the plant biomass at 2 cm above-ground on four 50 cm × 50 cm plots on all treatment plots. Plant biomass was dried at 80°C for 48 hr and weighed to the nearest gram. The four values per plot were then summed and given as g/m^2. In 2015, we measured below-ground biomass immediately after cutting the above-ground biomass. We took four soil cores (0–10 cm depth, diameter of 5.6 cm) per treatment plot and sieved the soil to collect roots and stones >2 mm. We washed the attached soil material from the roots and subsequently dried all root fragments until constant weight at 60°C (minimum 72 hr). We weighed the dried roots and transformed the below-ground biomass to g/m^2 using the diameter of the soil corer. Due to the very labour-intensive methods required for taking root biomass measurements, we decided to measure them in the first season after the disturbance only, where impacts of the sward disturbance were expected to be most pronounced.

2.4 | Soil nutrients

We used ion-exchange resin bags (Sibbesen, 1977; Skogley & Dobermann, 1996), i.e. nylon bags containing anion/cation mixed-bed resin beads, plus specific resin beads for anionic heavy metals and phosphate (TerrAquat, Nürtingen, Germany), to measure nutrient availability in terms of nitrate (NO_3-N), ammonium (NH_4-N), potassium (K) and phosphate (PO_4-P) concentrations in situ. Each resin bag with a diameter of 5 cm contained 19.5 g of dry resin. Four months after experimental sward disturbance, we installed a total of 438 bags (three replicates with a minimum distance of 6 m in all treatment plots) at 20 cm depth. We left the bags in the soil from March to early August 2015, approximately 145 days.

After removal, we stored the resin bags in a refrigerator. We extracted the nutrients for each bag separately. With 100 ml of 1 M NaCl we extracted 15 g of moist resin in two steps. In each step, we used 50 ml and shook it for 30 min before filtering it. We measured NH_4-N and NO_3-N concentrations with a Continuous Flow Auto Analyser (Skalar Analytic GmbH, The Netherlands) and K concentrations with a Spectro ARCOS ICP-OES (Spectro Analytical Instruments, Kleve, Germany). After applying a standard Fassel-type torch (inner diameter: 1.8 mm) in axial position for the elemental determination, we introduced the samples into a cross flow nebulizer and a Scott spray chamber. As nebulizer gas we used argon with a flow rate of 0.8 L/min, as auxiliary plasma gas we used argon with a flow rate of 0.85 L/min and as cooling gas we used argon with a flow rate of 12.0 L/min. The radio frequency was 1,400 W and we selected the most sensitive wavelengths. We measured samples either directly or after diluting them 1:10 in ultra-pure water (Millipore Milli-Q system, Schwalbach, Germany). We extracted PO_4-P in an additional 15 g sample of moist resin using 100 ml 0.5 M H_2SO_4 and measured it following the same protocol as described above. We state all concentrations as mean values per treatment plot in μg/g (dry weight) resin. In four plots NO_3-N values were below the detection limit. As total absence of the respective nutrient is unlikely, we set NO_3-N concentration values at 10% of the lowest measured value. Due to the very labour-intensive methods, we decided to measure soil nutrients in the first season after the disturbance only, where impact of the sward disturbance was expected to be most severe.

2.5 | Soil moisture

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

2.6 | Trait data

We used specific leaf area (SLA), the occurrence of a bud bank and lateral spread as species-specific functional traits to assess the functional composition of plant communities. Traits were derived from the databases TRY (Kattge et al., 2011) and CLOPLA (Klimešová & Bello, 2009). In a pre-analysis, SLA proved to be almost identical with the first axis of a principle component analysis of resource economic strategy formed by SLA (Cerabolini et al., 2010; Kleyer et al., 2008; Wright et al., 2004), leaf dry matter content (Cerabolini et al., 2010; Kleyer et al., 2008) and leaf N (Cerabolini et al., 2010; Fitter & Peat, 1994; Kleyer et al., 2008; Wright et al., 2004). The bud bank was considered absent (value = 0) when species had fewer than 10 buds between 0 and 10 cm below-ground and present (value = 1) when species had more than 10 buds between 0 and 10 cm below-ground. Lateral spread was recorded as absent (value = 0), when species did not possess clonal organs for horizontal growth of at least 0.25 m/year and present (value = 1), when species possessed clonal organs for horizontal growth of at least 0.25 m/year. For all three traits, we calculated community-weighted means (CWM) according to the cover of each species, using the vegetation records of the control plots in 2015, i.e. in the first season. We used the same data to calculate functional richness with the package FD version 1.0-12 (Laliberté & Legendre, 2010), without accounting for the abundance of the individual species.

Further, we included the seed bank in addition to the functional traits. In October 2014, we took five soil samples of a depth of 10–15 cm in all treatment and control plots, resulting in 10 samples per grassland site and later on observed germination of seeds in the soil bank at the Botanical Garden of the University of Bern, Switzerland. More information on the methodology is given in the Supplementary Material S1.

2.7 | Statistical analysis

Firstly, we tested the effect of region and disturbance on above- and below-ground plant biomass, plant cover, plant species richness and the availability of NO_3-N, NH_4-N, K and PO_4-P using linear mixed models with site as a random factor (package lme4: Bates, Mächler, Bolker, & Walker, 2015). For plant biomass, we also included the day of the year of biomass collection as an explanatory variable. Variables were transformed (either log- or square-root-transformation) if necessary to achieve a normal distribution of their residuals.

Secondly, we calculated log response ratios, hereafter called lnRR or relative recovery and relative nutrient release respectively, by taking the logarithm of the non-transformed response variables of the disturbance plot divided by the response variables of the control plot. An lnRR of zero means complete recovery of plant communities and nutrient release after the disturbance, whereas a negative lnRR indicates incomplete recovery of plant communities or a decreased nutrient release. A positive lnRR indicates increased ecosystem function of plant communities or increased release of nutrients after the disturbance. We also calculated the difference (treatment – control) as absolute recovery and absolute nutrient release, to test whether results differ when absolute rather than relative values are considered, as most studies focus on relative recovery only, which might lead to us overlooking biologically important results of applied interest caused by initial differences of the studied systems.

Thirdly, we fitted linear models including LUI, resident species richness, soil water content, the three CWM functional traits and number of seedlings from the seed bank as explanatory variables, to assess the importance of these variables for relative and absolute recovery of plant communities and nutrient release. To account for regional effects and environmental co-variates that varied within region, we calculated a linear model for each variable including the three regions, soil pH, topographic wetness index (TWI; Sørensen, Zinko, & Seibert, 2006) and soil depth of the grasslands and used the standardized residuals of these models for analyses. Further, we calculated the same linear models using functional richness instead of CWM functional traits and number of seedlings from the seed bank (Table S1), to decide which variables should be included in the fourth step, the structural equation models (SEMs).

Fourthly, we used SEMs to analyse the direct and indirect effects of resident species richness and LUI on the relative and absolute recovery of plant communities and nutrient release respectively (Figure S1). In the SEMs, LUI and plant species richness were directly linked to absolute and relative recovery to test their direct effects (Figure S1). LUI was additionally linked to resident species richness to analyse whether LUI also indirectly affected recovery via resident species richness. We hypothesized that part of the effect of LUI and resident species richness on recovery is mediated by functional composition and recolonization from the seed bank. However, the linear models showed that neither the CWM functional traits, nor the number of seedlings from the seed bank strongly and consistently influenced absolute or relative recovery (Table S1). Therefore, we decided to test the indirect effect of LUI and resident species richness on recovery via functional composition by using functional

richness only. With the reduced plant cover after the disturbance, we expected soil water content to potentially influence recovery. We therefore included soil water content as an additional environmental variable, which correlates with LUI and directly influences recovery. We calculated separate models for 2015 and 2016 and the absolute and relative recovery of plant communities and nutrient release.

Running our SEMs for both absolute and relative recovery and separately for the years 2015 and 2016 resulted in a total of 24 models. We also fitted a SEM with a correlation between resident species richness and CWMs, rather than a directed path from resident species richness to the CWMs. Although the significance of some effects changed in these SEMs, the overall pattern remained the same as in the models presented in the results.

3 | RESULTS

3.1 | Effects of disturbance on plant communities and nutrient release

After the disturbance, regrowth of plants occurred from seed germination and resprouting of plant roots and fragments. Despite some newly emerging plant species, most of the species found in the disturbed plots were also present in the control plots (Figure S2). An overview of the gradient of LUI and species richness as well as the variation of the treatment effects, as calculated with a log response ratio (ln(disturbed plot/control plot)), is given in Figure S3.

In the first season, approximately half a year after the experimental sward disturbance, species richness was increased across all grassland sites by 11% (Figure 1a), while plant cover (–44%, Figure 1b), above-ground biomass (–54%, Figure 1c) and below-ground biomass (–64%, Figure 1d) were decreased. NO_3-N in soil was increased by 140% (Figure 2a), while NH_4-N (–39%, Figure 2b), K (–35%, Figure 2c) and PO_4-P (–38%, Figure 2d) were reduced. This means that sward disturbance substantially affected all response variables in the first season. In the second season after the disturbance, approximately one and a half years after the experimental sward disturbance, we found that across all grassland sites, species richness was still increased by 12% (Figure 1e), while plant cover (Figure 1f) and above-ground biomass (Figure 1g) were no longer affected by disturbance. Soil nutrient concentrations and below-ground biomass were not measured in the second season.

We found some regional differences in the treatment effects (Table S2; Figure S4). We found that above-ground biomass (Figure S4a), plant cover (Figure S4b), plant species richness (Figure S4c) and release of NO_3-N in the first season (Figure S4d) and above-ground biomass (Figure S4e) and plant species richness in the second season (Figure S4g) reacted in the same direction in all regions, although the responses varied in strength. However in the second season disturbance had different effects on plant cover in the regions, leading to overall disappearance of the effect of disturbance on plant cover (Figure S4f). In the second season after the disturbance, plant cover was still reduced in the disturbance plots in the Schwäbische Alb and Hainich-Dün but increased in Schorfheide-Chorin (Figure S4f).
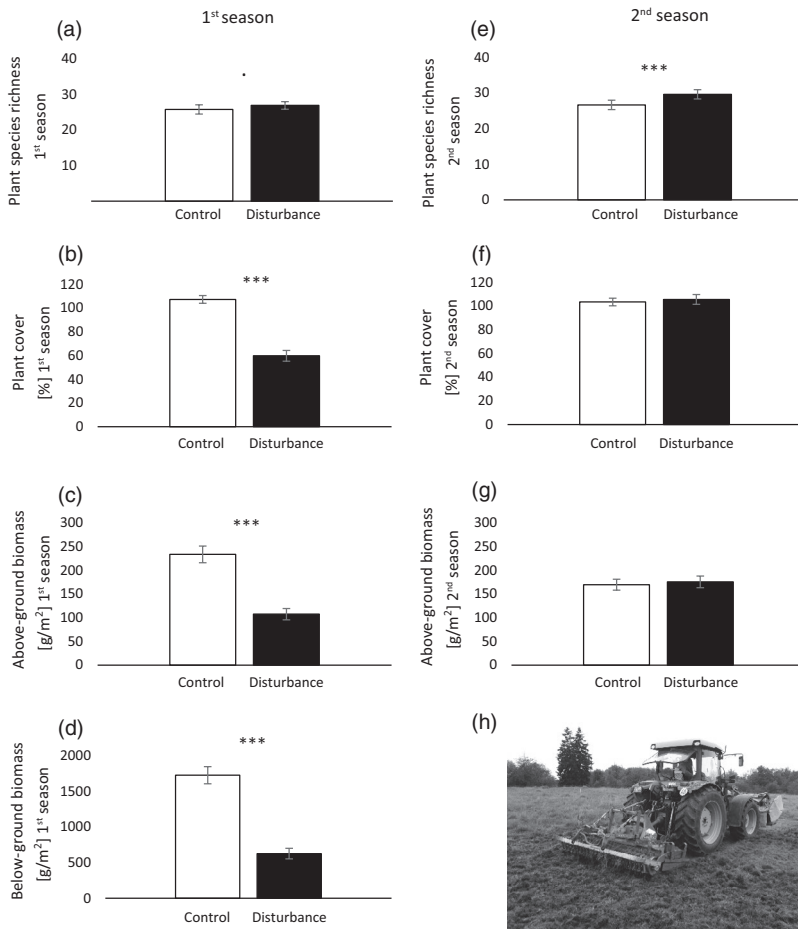
FIGURE 1 Effects of sward disturbance on plant communities in 73 grasslands differing in land-use intensity. Mean values over all three study regions of (a) plant species richness of the first season, (b) plant cover of the first season, (c) plant above-ground biomass (g/m^2) of the first season, (d) below-ground 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 above-ground 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). · indicates a p-value between 0.1–0.05, * indicates a p-value between 0.05–0.01, ** indicates a p-value between 0.01–0.001, *** indicates a p-value between 0.001–0.0001
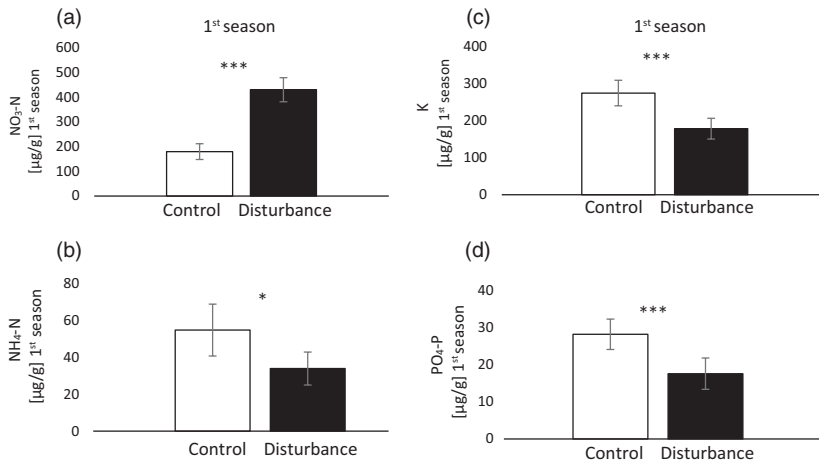

FIGURE 2 Effects of sward disturbance on nutrient availability in 73 grasslands differing in land-use intensity. Mean values over all three study regions of (a) NO_3-N, (b) NH_4-N, (c) K, and (d) PO_4-P according to the different treatments. · indicates a p-value between 0.1–0.05, * indicates a p-value between 0.05–0.01, ** indicates a p-value between 0.01–0.001, *** indicates a p-value between 0.001–0.0001

3.2 | Recovery as affected by functional composition

Testing the importance of the CWM traits SLA, lateral spread and bud bank, as well as the number of seedlings from the seed bank for recovery of plant communities and nutrient release showed that none of them had strong effects (Table S1). As none of the single trait analysis showed markedly better results, we used functional richness as a simplification in the SEMs reported hereafter.

Relative recovery of plant cover (Figure 3b), above- (Figure 3c) and below-ground biomass (Figure 3d; marginally significant), but also relative release of NO_3-N (Figure 5a) and NH_4-N (Figure 5b) were increased in grasslands with high functional richness in the first season after the disturbance. In the second season after the disturbance, grasslands with high functional richness showed decreased relative recovery of plant cover (Figure 3f). For absolute recovery, only above- (Figure 4c) and below-ground biomass (Figure 4d) were higher in grasslands with high functional richness than in grasslands with low functional richness, in the first season after the disturbance.

Overall, grasslands with high functional richness had increased relative and, partly, absolute recovery of plant communities (Table S3), but also increased relative nutrient release (Table S4) after the
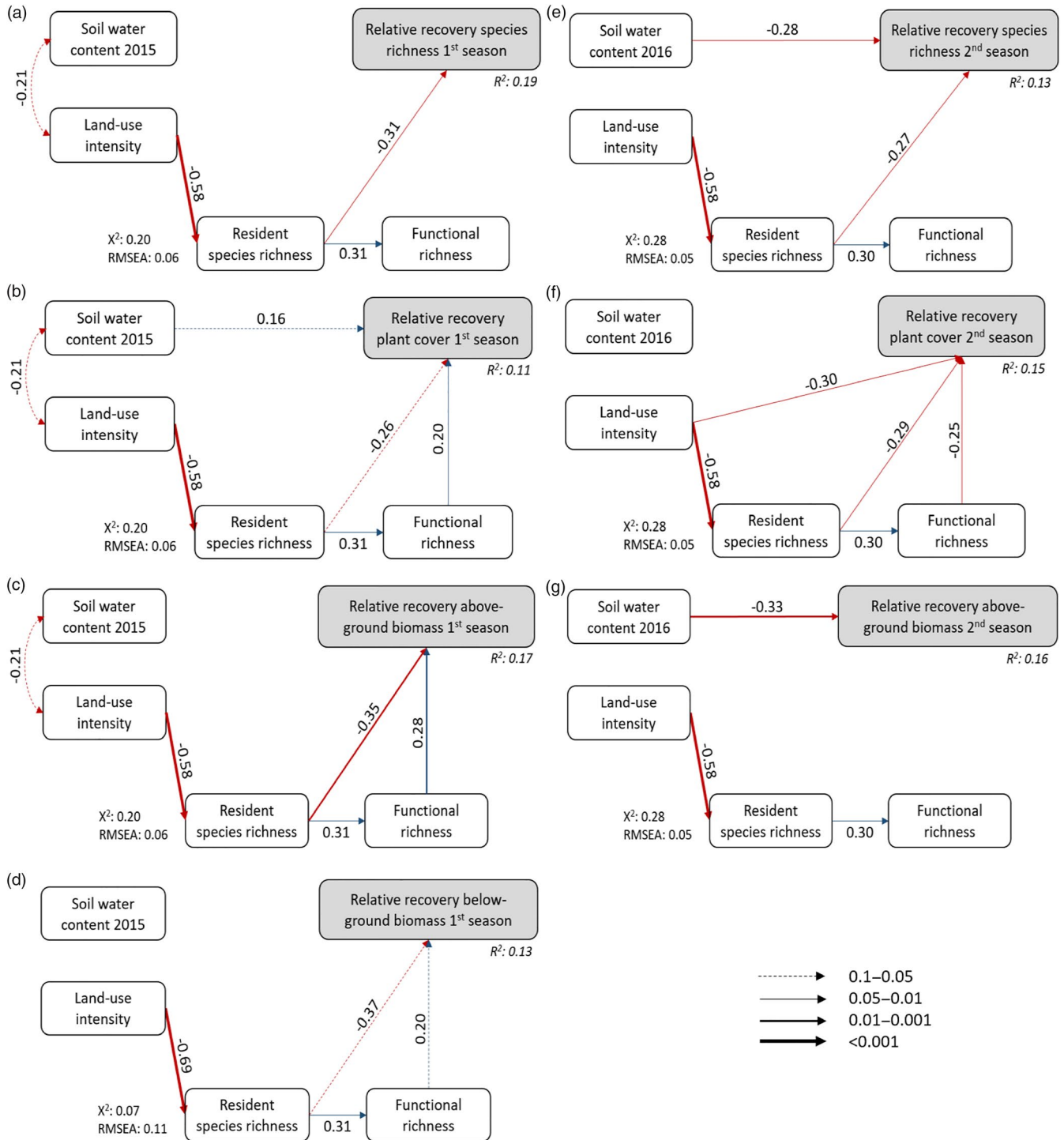
FIGURE 3 Structural equation models showing direct and indirect effects of different drivers of relative recovery, calculated as ln(disturbance/control), for plant species richness and plant related ecosystem functions in the (a–d) first and (e, f) second season after the disturbance. The R^2 of the response variable 'relative recovery' is given for each SEM. Further, for each SEM the p-value of the model fit parameter χ^2 and the root mean square error of approximation RMSEA ($p > 0.05$ and RMSEA < 0.08 indicate good model fit) are given

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

3.3 | Recovery as affected by resident species richness

Using SEMs to distinguish direct and indirect effects of resident species richness on recovery of plant communities and release of
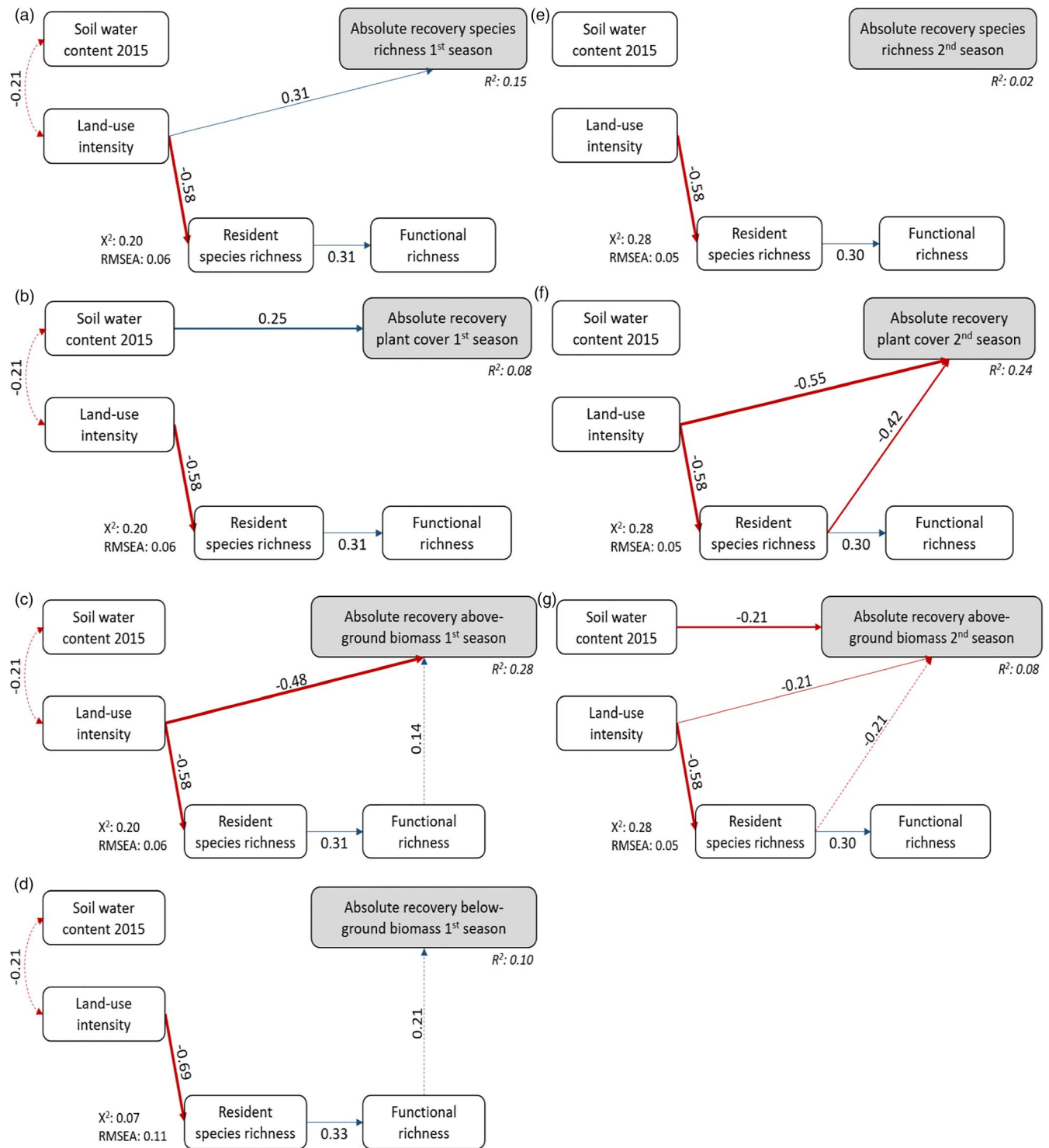
FIGURE 4 Structural equation models showing direct and indirect effects of different drivers of absolute recovery, calculated as ln(disturbance - control), for plant species richness and plant related ecosystem functions in the (a–d) first and (e–g) second season after the disturbance. The R^2 of the response variable 'relative recovery' is given for each SEM. Further, for each SEM the p-value of the model fit parameter χ^2 and the root mean square error of approximation RMSEA ($p > 0.05$ and RMSEA < 0.08 indicate good model fit) are given

nutrients after sward disturbance, revealed that relative recovery of plant species richness (Figure 3a), plant cover (Figure 3b; marginally significant), above- (Figure 3c) and below-ground biomass (Figure 3d; marginally significant) were lower in grasslands with

high resident species richness than in grasslands with low resident species richness. This was still the case for the relative recovery of species richness (Figure 3e) and plant cover (Figure 3f) in the second season after the disturbance. Further, resident species richness
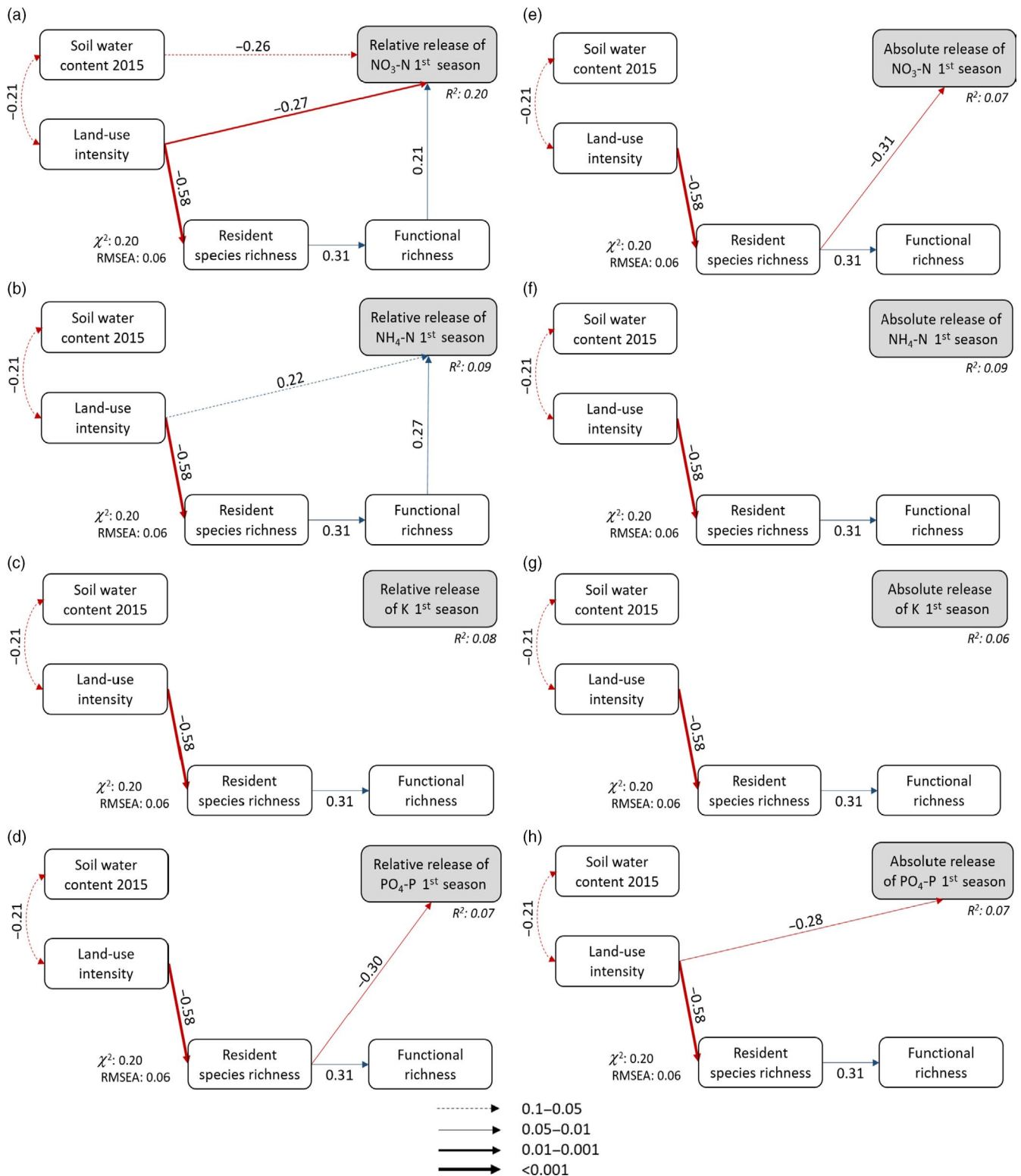
FIGURE 5 Structural equation models showing direct and indirect effects of different drivers of (a–d) relative (ln(disturbance/control)) and (e–h) absolute (disturbance – control) recovery of nutrient release after the disturbance. The R^2 of the response variable 'relative recovery' is given for each SEM. Further, for each SEM the p-value of the model fit parameter χ^2 and the root mean square error of approximation RMSEA ($p > 0.05$ and RMSEA < 0.08 indicate good model fit) are given

indirectly increased the relative recovery of plant cover (Figure 3b), above- (Figure 3c) and below-ground biomass (Figure 3d) in the first season after the disturbance by increasing the functional richness in the respective grassland communities. For relative nutrient release, resident species richness only played a minor role compared with its role for the relative recovery of plant communities (Figure 5a–d).

Grasslands of high resident species richness had lower release of PO_4-P than grasslands of low resident species richness (Figure 5d), while high resident species richness indirectly increased the release of NO_3-N and NH_4-N via increasing functional richness (Figure 5a,b).

Absolute recovery of plant communities was influenced much less by the resident species richness of grasslands than was relative recovery of plant communities. For the first season after the disturbance, only the indirect positive effect of resident species richness on absolute recovery of above- (Figure 4c) and below-ground biomass (Figure 4d) via increasing functional richness was significant. In the second season after the disturbance, grasslands with high resident species richness had lower absolute recovery of plant cover (Figure 4f) and above-ground biomass (Figure 4g; marginally significant) than grasslands of low resident species richness. For absolute nutrient release, resident species richness also only played a minor role (Figure 5e–h). Grasslands with high resident species richness merely had lower absolute release of NO_3-N than grasslands of low resident species richness (Figure 5e).

Overall, high resident species richness strongly decreased the relative recovery of plant communities (Table S3), while it only played a minor role for the absolute recovery of plant communities (Table S3) and relative and absolute nutrient release (Table S4). This was also supported by the standardized total effects, which additionally showed that the influence of resident species richness on relative and absolute recovery was rather direct than indirect via functional richness (Figure S5).

3.4 | Recovery as affected by land-use intensity

Using SEMs to distinguish direct and indirect effects of LUI, we found that LUI directly affected relative recovery of plant cover in the second season only (Figure 3f), where high-intensity grasslands had lower recovery of plant cover than low-intensity grasslands. However, high LUI also led to plant communities with lower resident species richness. Therefore, high LUI indirectly increased the relative recovery of plant communities by decreasing negative effects of high resident species richness (Figure 3). Relative nutrient release was decreased for NO_3-N and increased for NH_4-N in high-intensity grasslands compared with low-intensity grasslands (Figure 5a,b).

Absolute recovery of plant communities was influenced more directly by LUI than relative recovery. Compared with low-intensity grasslands, grasslands with high LUI had increased absolute recovery of species richness (Figure 4a) and decreased absolute recovery of above-ground biomass (Figure 4c) in the first season after the disturbance and decreased absolute recovery of plant cover (Figure 4f) and above-ground biomass (Figure 4g) in the second season after the disturbance. LUI also indirectly increased absolute recovery of plant cover (Figure 4f) and above-ground biomass (Figure 4g) in the second season via decreasing negative direct effects of resident species richness. Absolute nutrient release of PO_4-P was the only measured nutrient that was directly affected by LUI, where high-intensity grasslands had lower release of PO_4-P than low-intensity grasslands (Figure 5h). High-intensity grasslands also had increased absolute release of NO_3-N due to an indirect effect via decreased resident plant species richness (Figure 5e).

Overall, high LUI frequently increased the relative recovery of plant communities indirectly via decreasing resident species richness, but directly decreased the absolute recovery of some aspects of plant communities (Tables S3). In addition, LUI had only minor effects on relative and absolute nutrient release (Table S4). If standardized total effects were considered, the importance of LUI for absolute and relative recovery became more apparent (Figure S5). This importance seemed therefore to be largely of an indirect nature, via changing resident species richness and functional richness.

4 | DISCUSSION

4.1 | Effects of disturbance on plant communities and nutrient release

In the first growing season, the effect of experimental sward disturbance on plant communities (Figure 1) and nutrient release (Figure 2) was very strong on all 73 grassland sites. While disturbance drastically reduced above- and below-ground biomass and plant cover in the first season, it increased plant species richness. This increase in species richness was found in more intensively managed grasslands with low resident species richness, which are not comparable with the natural, high diversity communities studied by Hirst, Pywell, Marrs, and Putwain (2003) and Biswas and Mallik (2010). The comparable low-intensity grasslands with high resident species richness experienced a decrease in species richness, which was also found in these previous studies. The increase of species richness in grasslands managed at high intensity was most likely due to reduced plant cover and therefore reduced light competition after the disturbance. Hautier, Niklaus, and Hector (2009) previously showed that increased competition for light could indeed lead to biodiversity loss. Further, the reduced plant cover allowed 'new' species to establish from the seed bank or seed rain (see also Klaus et al., 2017; Klaus, Hoever, et al., 2018a). Including a wide gradient of resident species richness among our studied grasslands (12–70 species on a 4 m × 4 m plot; Figure S3) enabled us to show that the effect of a disturbance depended on the initial state of the grasslands.

After the first season, disturbance effects disappeared for above-ground biomass and plant cover and, on some sites, values from disturbed plots even exceeded those of the control plots, probably due to compensatory growth stimulated by disturbance-related release of nutrients (especially NO_3-N, see below; McNaughton, Wallace, & Coughenour, 1983; Klaus, Kleinebecker, et al., 2018b).

Disturbance affected the release of soil nutrients in the first season after the disturbance in different ways. NO_3-N was strongly increased and NH_4-N, mobile K and PO_4-P were decreased. The increase of NO_3-N was most likely caused by increased activity of soil organisms making use of dead plant matter (e.g. plant litter, fine and coarse roots; Six, Conant, Paul, & Paustian, 2002). In addition, mechanical perturbation might have disrupted soil aggregates and released protected organic matter (Cuevas, Mastrantonio, Ojeda, &

Jaksic, 2012). This is in line with previous studies showing severe nitrate leaching into ground water as one consequence of mechanical sward disturbance (e.g. Whitmore, Bradbury, & Johnson, 1992). The decreased release of NH_4-N was presumably due to the immediate nitrification caused by increased air volume in the disturbed soil or due to fast processing of ammonia by ammonia oxidizing microorganisms (Jha, Kashyap, & Singh, 1996). The decreased release of K and PO_4-P concentrations might have been caused by reduced mobilization of especially P due to reduced plant activity (e.g. via root exudation). Further, an increased uptake of these elements by soil microorganisms (living in the topsoil above the resin bags) either due to increased microbial abundance (Lamb, Kennedy, & Siciliano, 2011) and/or changes in microbial community structure (Hendrix et al., 1986) might have been important. These mechanisms could have been driven by the simultaneous increase in available NO_3-N and easily available labile organic matter.

4.2 | Relative importance of functional community composition, resident species richness and land-use intensity for recovery

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

4.2.1 | Functional composition

The different plant traits characterizing mean functional community composition hardly explained the recovery of ecosystem functions. The low importance of specific functional traits for the recovery of ecosystem functions is in contrast with previous studies, where CWM traits were found to explain variation in ecosystem functions (Allan et al., 2015; SLA), stability of communities (Fischer et al., 2016; PCA including several traits) or stability of populations (Májeková, Bello, Doležal, & Lepš, 2014; LDMC, rooting depth and leaf δ^{13}C; Busch et al., 2018; PCA including several traits). While some of these differences could be due to the consideration of different CWM traits or stability measures, there is also an alternative explanation. Our wide gradient in land-use intensity may have masked effects of CWM traits. For instance, grasslands with high CWM SLA recovered better, but these grasslands are mostly restricted to high land-use intensity and not enough variation in CWM SLA was left after accounting for land-use intensity. Thus, we suggest that in agricultural grassland communities, where the diversity and functional composition of communities are strongly influenced by management, effects of CWM traits might be overridden (Grace et al., 2007).

Functional richness increased the recovery of several ecosystem functions in the first season after the disturbance, which is in line with previous studies (Díaz & Cabido, 2001; Laliberté et al., 2010; Mori, Furukawa, & Sasaki, 2013; Weigelt, Schumacher, Roscher, & Schmid, 2008). Complementarity of plant species with different functional traits within a community can increase the chances of having species capable of coping with changed biotic and abiotic conditions after a disturbance, leading to a better recovery of ecosystem functions (insurance hypothesis; Yachi & Loreau, 1999). Next to increasing recovery of plant communities, higher functional richness also increased the relative release of NO_3-N and NH_4-N in the disturbed plots compared to the controls, most likely due to the loss of plant species with diverse N acquisition strategies. Furthermore, functionally rich plant communities (including leguminous herbs) (Hooper & Vitousek, 1998; Scherer-Lorenzen, Palmborg, Prinz, & Schulze, 2003) might favour functional diverse soil microbial communities due to more diverse organic N resources.

Altogether, these results suggest that while increasing the CWM of a specific functional trait does not necessarily lead to high stability of ecosystem functions in agricultural grasslands, increasing functional richness has the potential to buffer effects of disturbance on vegetation-related ecosystem functions with the drawback of increased release of nutrients in the soil.

4.2.2 | Resident species richness

Grasslands of high resident species richness had lower relative recovery of plant species richness, plant cover, plant biomass (first season only) and PO_4-P than grasslands of low resident species richness. Overall, our findings thus seem to disagree with results from the literature, which often report positive effects of species richness on stability (Frank & McNaughton, 1991; McGrady-Steed, Harris, & Morin, 1997; Naeem & Li, 1997; Tilman, Reich, & Knops, 2006). This discrepancy can have several explanations. One difficulty relates to the various definitions and aspects of stability of ecosystems (Grimm & Wissel, 1997; Hodgson, McDonald, & Hosken, 2015; Ingrisch & Bahn, 2018; Nimmo, Nally, Cunningham, Haslem, & Bennett, 2015). In our study, we considered recovery, i.e. how far ecosystem functions returned to initial conditions. Previous studies focusing on stability concepts such as resilience, recovery and resistance also found no or negative effects (DeBoeck et al., 2018; Isbell et al., 2015). However, previous studies reporting positive effects of species richness on stability, considered other stability measures, such as resistance (Frank & McNaughton, 1991; Isbell et al., 2015) or variability over time (McGrady-Steed et al., 1997; Naeem & Li, 1997; Tilman et al., 2006). Therefore, rather than generally contradicting a positive species richness-stability relationship, we found that grasslands with high species richness suffered more strongly from the disturbance and therefore showed lower stability in regard to the specific stability concept of relative recovery.

A further difference between our study and previous studies is the type and especially the strength of the disturbance considered. Compared with mostly, relatively mild climatic disturbances, as considered for example by Isbell et al. (2015), our mechanical disturbance was very severe. It affected not only the growth of the plants but killed plant species and reshaped the entire vegetation. Such a severe disturbance is more similar to the disturbances included in the meta-analysis by DeBoeck et al. (2018). They found, similar to

our study, that high species richness does not always buffer the consequences of extreme disturbances. They suggest that the influence of species richness can depend on the community assembly processes involved, differences in ecosystem sensitivity to disturbances or on the specific characteristics of the studied disturbances (DeBoeck et al., 2018).

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

4.2.3 | Land-use intensity

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

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

High land-use intensity also had a positive effect, namely on absolute species richness after the disturbance. This can be explained by increased light availability, which promoted weak competitors (Hautier et al., 2009), an effect that was likely to be stronger in grasslands with high land-use intensity, where plant biomass was initially high and plant cover dense. Furthermore, simple plant communities consisting of 12 plant species are more likely to regenerate than more complex communities consisting of 60 plant species. We also found that low-intensity grasslands had a larger relative increase of released NO_3-N compared with grasslands with high land-use intensity, which was very likely caused by the already high release of NO_3-N in grasslands with high land-use intensity even without the presence of a disturbance (Klaus, Kleinebecker, et al., 2018b).

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

4.2.4 | Absolute versus relative recovery

The differences between the drivers of absolute versus relative recovery were most pronounced for land-use intensity and resident plant species richness for the recovery of plant cover and above-ground biomass. These two ecosystem functions are the ones that farmers try to maximize in agricultural grasslands and therefore their initial levels correlate most strongly with land-use intensity. Absolute recovery does not account for differences in initial conditions, therefore grasslands with high initial ecosystem functions (i.e. high biomass, high plant cover) showed lower recovery, at least on the short-term. While the relative recovery enabled us to study the effects of our explanatory variables on recovery independent of their initial absolute differences among grasslands and resulted in more mechanistic findings, absolute recovery helped to understand the meaning of a disturbance for the system when starting conditions vary widely and therefore resulted in more applied findings.

5 | CONCLUSIONS

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

AUTHORS' CONTRIBUTIONS

D.P., N.H. and M.F. conceived and designed the experiment; D.S., V.H.K., T.K., I.S., S.W., R.S.B., S.M., E.K., J.H., S.N. and U.H. collected and contributed to the data; D.S., V.H.K., N.H., M.F. and D.P. analysed the data and drafted the manuscript. All authors helped to revise the manuscript and gave final approval for publication.

DATA ACCESSIBILITY

Data are available in the BExIS database of the Biodiversity Exploratories program https://www.bexis.uni-jena.de/PublicData/About.aspx (Datasets: 19810, 19811, 19812, 20037, 20446, 21867, 20426, 20646, 20666). The datasets with the ID 19810, 19811, 19812, 20037, 20446, 21867 will be publicly available under the URL https://www.bexis.uni-jena.de/PublicData/About.aspx from autumn 2019, the datasets with the ID 20426, 20646, 20666 will be publicly available under the URL https://www.bexis.unijena.de/PublicData/About.aspx from autumn 2020 on. Until then, data is available upon request (bexis@uni-jena.de).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.