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RESEARCH ARTICLE

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Grazing-induced patchiness, not grazing intensity, drives plant diversity in European low-input pastures

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Abstract

1. Livestock grazing at low stocking rates is widely recommended to maintain grassland biodiversity. However, empirical evidence of grazing-intensity effects on plant diversity is contradictory. Explicitly considering the small-scale heterogeneity of short, frequently grazed and tall, rarely grazed patches typical of low-input grazing systems may be crucial to the understanding of paddock-scale grazing effects.
2. We studied three patch types (short, intermediate, tall) within an unfertilised long-term cattle grazing experiment in Lower Saxony, Germany, comparing three paddock-scale grazing intensities. We analysed soil nutrient concentrations and recorded vegetation composition at a total of 135 plots. We determined species richness, Simpson diversity, Simpson evenness and beta diversity of individual plots (plot scale) and patch types within paddocks (patch scale). To quantify paddock-scale diversity, we resampled plot-scale species composition across a gradient of relative proportions of short and tall patches within a paddock.
3. Patch type, not paddock-scale grazing intensity, was the main driver of plant diversity at both plot and patch scale. Short patches were more diverse than tall patches, but the effect was not strongly mediated by the lower soil nutrient concentrations in the short patches. By contrast, both patch type and grazing intensity affected vegetation composition at plot and patch scale.
4. Beta-diversity within and between patch types was independent of grazing intensity; consequently, paddock-scale diversity was determined by the relative proportion of short versus tall patches. Higher alpha diversity of short patches compared to tall patches was more important than beta diversity between the two patch types in shaping paddock-scale diversity. Consequently, with increasing short-patch proportion, paddock-scale diversity increased.
5. *Synthesis and applications*. Our study identifies the grazing-induced patch structure as the most important driver of plant diversity across different grazing intensities in low-input, that is, unfertilised and continuously stocked, pastures. To optimise grazing management for biodiversity, understanding plant-diversity responses to grazing at the patch scale is indispensable. Our results suggest that, in unfertilised, continuously stocked European pastures, trade-offs between biodiversity and

agronomic production may be small, as short patches, whose proportion increases with stocking rate, also had the highest plant diversity.

KEYWORDS
biodiversity, grassland, micro-scale pattern, patch grazing, patch structure, soil nutrients, spatial heterogeneity, stocking rate

1 | INTRODUCTION

Grasslands are an important European ecosystem, covering over 900,000 km^2 within the EU-28 (EUROSTAT, 2017). Only few of these grasslands represent the natural vegetation; the majority has their origin in some form of human utilisation (Poschlod, Baumann, & Karlik, 2009). Nevertheless, these grasslands harbour great plant diversity: Many are recognised as Natural Habitat Types of Community Interest within the Natura 2000 framework (Council Directive 92/43/EEC), and grasslands make up at least one third of the EU high-nature value farmland area (Paracchini et al., 2009). This biodiversity is under threat through two contrasting developments (Ostermann, 1998): In many areas, fertilisation and high utilisation intensity cause diversity losses, while low economic performance leads to abandonment and subsequent woody succession at grassland sites of low productivity (Isselstein, 2018; Poschlod et al., 2009). An extensive management, especially in the form of grazing, is therefore widely recommended to preserve grassland diversity, while maintaining economic feasibility (Rook & Tallowin, 2003), and both lower and upper limits for stocking rates are common elements of agri-environmental schemes in grasslands (Primdahl, Peco, Schramek, Andersen, & Oñate, 2003). This management recommendation is supported by ecological theory that predicts plant diversity to peak at intermediate grazing intensities (Cingolani, Noy-Meir, & Diaz, 2005; Milchunas, Sala, & Lauenroth, 1988). A recent meta-analysis, however, pointed out the scarcity of studies in which different grazing intensities, rather than exclosures and grazed areas, are compared (Herrero-Jáuregui & Oesterheld, 2018). In the existing studies, effects of grazing intensity on diversity could be either positive or negative and were mostly small in magnitude (Herrero-Jáuregui & Oesterheld, 2018). As both grassland managers and policy makers depend on evidence-based guidelines for deciding on appropriate stocking rates, a better understanding of the mechanisms through which grazing intensity affects plant diversity is required.

Achieving such understanding is complicated by the pronounced spatial heterogeneity found in grazed grasslands (Adler, Raff, & Lauenroth, 2001). Extensive grazing systems are characterised by low stocking rates, typically in the form of long stocking periods at low animal density, an absence of fertilisation and limited, if any, additional mowing operations. Under such conditions, positive feedbacks between defoliation and forage quality typically lead to a mosaic structure of short, frequently grazed, and tall, rarely grazed patches. At first, such positive feedbacks can be based on the higher digestibility of biomass regrowth within the same vegetation period (Bakker, Leeuw, & Wieren, 1983; Cid & Brizuela, 1998). Over time, the initial patch grazing pattern can remain relatively stable in temperate livestock grazing systems (Bakker et al., 1983; Cid & Brizuela, 1998; Tonn, Raab, & Isselstein, 2018; Willms, Dormaar, & Schaalje, 1988), causing vegetation development to diverge between short and tall patches (Cid & Brizuela, 1998; Ludvíková, Pavlů, Pavlů, Gaisler, & Hejcman, 2015), which may reinforce the pattern (Adler et al., 2001).

Short and tall patches of a patch-grazing system are a small-scale combination of high and low grazing intensity within the same paddock, but in contrast to physically separated plots with different grazing intensities, they are connected via nutrient flows through animal dung and urine. Nutrient removal by grazing animals is determined by the grazing intensity and therefore higher in short than tall patches. By contrast, the pattern of nutrient return through urine and dung is the result of animal behaviour during both grazing and non-grazing periods. If non-grazing behaviour is independent from the patch-grazing mosaic, the ratio between nutrient removal and nutrient return will be larger in short than in tall patches, resulting in a net nutrient transfer from short to tall patches.

As a consequence of long-term differentiated defoliation regimes and nutrient balances in short and tall patches, the diversity of these two patch types should develop in different directions. Less frequent defoliation in tall patches will increase light limitation, while nutrient transfer from short to tall patches simultaneously reduces nutrient limitation in tall patches. As a shift from nutrient towards light limitation is a major mechanism of species loss in grasslands (Borer et al., 2014; Hautier, Niklaus, & Hector, 2009), tall patches should be less diverse than short patches.

Paddock-scale grazing intensity may have little effect on the defoliation and nutrient transfer regime experienced within one patch type. The grazing-intensity effect on paddock-scale diversity will then be driven by the way grazing intensity influences the relative proportions of short and tall patches (Cid & Brizuela, 1998; Tonn et al., 2018). Even if short patches are more species-rich than tall patches, the different growing conditions experienced in these two patch types should lead to considerable species turnover between them (Milchunas et al., 1988; Olff & Ritchie, 1998). Consequently, the highest paddock-scale plant diversity will occur at intermediate grazing intensities that result in the most balanced proportions of short and tall patches (Marion, Bonis, & Bouzillé, 2010).

To test these expectations, we studied plant diversity and composition in a more than 10-year-old cattle grazing experiment with three controlled paddock-scale grazing intensities, where a pronounced and temporally stable mosaic of short and tall patches had developed (Tonn et al., 2018). We considered three spatial scales: individual sampling plots, patch types within each paddock, and total paddocks (Figure 1). We hypothesised (H1) that plant diversity and composition at both plot and patch scale is driven by patch type, rather than by paddock-scale grazing intensity. Specifically, we expected (H2) that short patches would be more diverse than tall patches, and that this difference would at least partly be mediated by lesser soil nutrient concentrations under short patches. We further expected (H3) that paddock-scale grazing intensity drives paddock-scale plant diversity through its effect on the relative proportions of different patch types, and (H4) that the maximum paddock-scale diversity would be reached when these proportions were most evenly distributed.

2 | MATERIALS AND METHODS

2.1 | Study site and experimental design

We collected our data in a long-term grazing experiment in Relliehausen, Lower Saxony, Germany (centred at 51° 46′ 55″ N, 9° 42′ 10″ E, 175–230 m above sea level). Mean annual temperature during the study (2002–2014) was 8.8°C, and annual accumulated precipitation was 816 mm, based on the closest weather stations of the German Weather Service (Deutscher Wetterdienst; temperature: station Moringen-Lutterbeck, distance: 11.3 km; precipitation: until 2010 station Moringen-Lutterbeck, afterwards station Dassel/Solling, distance 2.0 km). The vegetation is old permanent grassland on a Vertic Cambisol. For at least ten years previous to the start of the experiment, the whole experimental area had formed one management unit that had been alternately grazed and cut without fertiliser application. The area has a west- to south-west-facing slope of 0–9°.

The experiment, established in 2002 (Isselstein, Griffith, Pradel, & Venerus, 2007) compares three intensities of cattle grazing defined by a target vegetation height: moderate grazing (6 cm), lenient grazing (12 cm) and very lenient grazing (18 cm target vegetation height). Each grazing intensity treatment was repeated three times in a randomised block design of nine 1-ha paddocks. The grassland received no fertiliser and was not cut, apart from occasionally removing invading shrubs. Simmental suckler cows grazed all three treatments from spring (end of April/beginning of May) to autumn (mid-September/mid-October). During this period, we measured vegetation height every two weeks in 50 locations per paddock, using a rising-plate meter (diameter 30 cm, weight 200 g; t'Mannetje, 2000). When measured vegetation height fell below the target, we removed some or all animals from the paddock; when target vegetation height was exceeded, we added animals to the respective paddocks. From 2005 to 2014, this resulted in an average of 462 (moderate), 262 (lenient) and 180 (very lenient) animal grazing days per hectare and year, standardised for an animal live weight of 500 kg. From 2002 to 2004, management of very lenient grazing treatment differed from later years, as vegetation was grazed to a target height of 12 cm using a traditional cattle breed.

2.2 | Sampling design

In each paddock, we sampled vegetation and soil parameters in three patch types: short, intermediate and tall. We defined these patch types as the lower, middle and upper third of the total 450

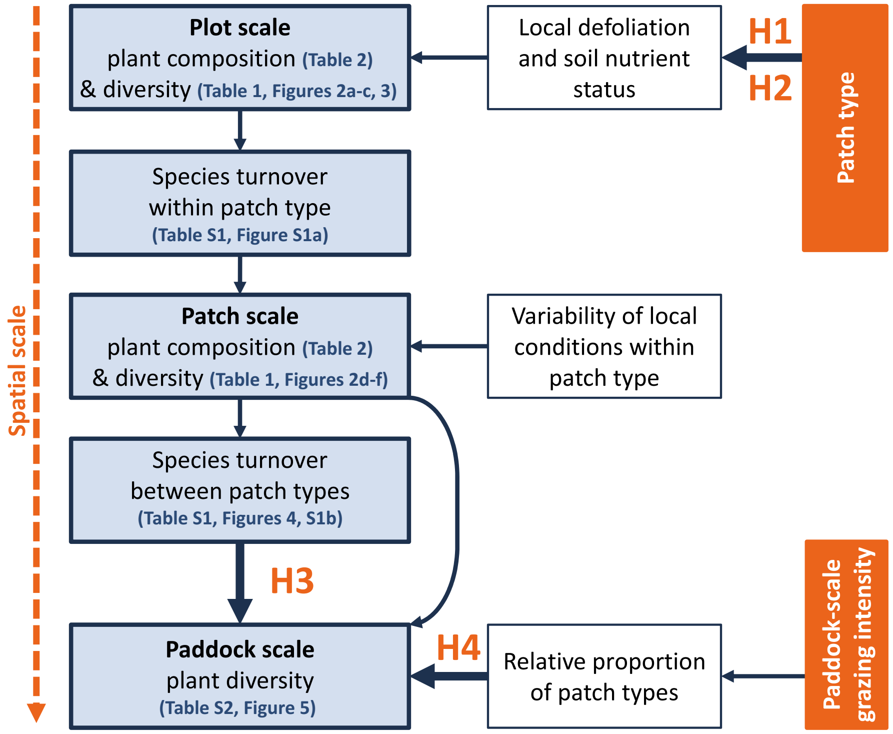

FIGURE 1 Conceptual graph showing the connection between parameters quantified in our study (shaded boxes, references to Figures and Tables showing the respective results) and the hypothesised main pathways through which plant diversity and composition at three spatial scales are influenced by patch type and by paddock-scale grazing intensity. H1–H4 refer to our hypotheses

fortnightly vegetation height measurements. This approach provided objective classification criteria while allowing for seasonal effects and fluctuations of mean vegetation height around the target value (Tonn et al., 2018). Based on a total of 34 measurement dates in 2013 and 2014, short patches made up 0.60, 0.31 and 0.17, and tall patches 0.15, 0.36 and 0.59 of the paddock area for moderate, lenient and very lenient grazing, respectively. During the two sampling periods of this study, the upper threshold for short patches was 6–10 cm and the lower threshold for tall patches 12.5–18 cm. We introduced the intermediate patch type in our sampling scheme because at intermediate plant heights there is considerable overlap between "functionally short", that is, frequently grazed, and "functionally tall", that is, rarely grazed vegetation (Rossignol, Chadoeuf, Carrère, & Dumont, 2011). Mean patch size (measured as mean minimum distance to the opposite patch type derived from a remote-sensing-based map) was 3.5, 1.7 and 1.5 m for short patches and 3.3, 6.0 and 10.1 m for tall patches under moderate, lenient and very lenient grazing (Tonn et al., 2018).

In each paddock, we randomly chose five locations to serve as the centre of a triplet of plots. Starting from this centre, we located one 0.5 m × 0.5 m plot per patch type (based on four rising-plate-meter measurements) by following a standardised random walk in order to avoid subjectivity in placing plots. This sampling design resulted in a total of 135 plots in 45 triplets. We sampled three triplets per paddock during peak standing crop in 2013 (11 June–6 August) and two more triplets per paddock in the following year (14 June–12 August).

2.3 | Diversity measures

On each plot, we recorded all higher plant species and visually estimated their relative abundance as the proportion of aboveground plant dry matter. We derived botanical composition and soil nutrient composition at the patch scale ($n = 27$) by aggregating plot-scale data ($n = 135$) for each paddock and patch type. For both scales, we determined species richness and calculated the reciprocal Simpson diversity index ($1/D$) and Simpson evenness ($E_{1/D}$) as:

$$1/D = 1/\left(\sum_{i=1}^{S} p_i^2\right) \tag{1}$$

$$E_{1/D} = \frac{1/D}{S} \tag{2}$$

where S is species number and p_i the relative abundance of species i.

We investigated β diversity for each paddock both at plot and at patch scale. Following the approach of Baselga (2009), we partitioned total dissimilarity (measured as Soerensen dissimilarity, β_{SOR}) into the two components of species turnover (measured as Simpson dissimilarity, β_{SIM}; species of one site are replaced by other species at another site) and species nestedness (β_{SNE}; species composition of one site is a subset of that of another site).

$$\beta_{SOR} = \beta_{SIM} + \beta_{SNE} \equiv \frac{b+c}{2a+b+c} = \frac{b}{b+a} + \left(\frac{c-b}{2a+b+c}\right)\left(\frac{a}{b+a}\right) \tag{3}$$

where a is the number of species two sites share, b is the number of species only occurring at the species-poorest and c the number of species only occurring on the species-richest site. At the patch scale, we determined the pairwise dissimilarity between each combination of the three patch types. At the plot scale, we calculated multiple-site dissimilarity between the five plots per patch type and paddock. We used the "betapart" package for these calculations (Baselga, Orme, Villeger, Bortoli, & Leprieur, 2018).

To test whether the effect of paddock-scale grazing intensity on diversity is mediated by its influence on the relative proportion of patch types, we resampled data from the 15 plots per paddock across varying proportions of plots from the short and tall patches. As our fortnightly vegetation height measurements in the years 2013 and 2014 revealed, the mean proportion of the intermediate height class was 0.27 with little variation between treatments. Accordingly, we kept the proportion of intermediate-patch-type plots in our samples constant. Each sample consisted of eight plots, of which two belonged to the intermediate patch type. The number of plots from short patches was varied from one to five and the number of plots from the tall patches, accordingly, from five to one. The sampling process was repeated to cover all possible combinations (50–1000, depending on the number of plots from short or tall patches). It yielded samples where the proportion of plots from either short or tall patch types ranged from 0.125 to 0.625, covering the range observed in the three grazing-intensity treatments in the field. We determined species richness, Simpson diversity and Simpson evenness for each sample and calculated average values for each paddock and patch-type composition.

2.4 | Soil parameters

We used extractable soil phosphorus (P) and potassium (K) as proxies for nutrient availability. Animal-mediated cycling of P and K in grazed grasslands is tightly coupled to that of N, the limiting nutrient in our experiment (N:P ratios 3.9–9.7 and N:K ratios 0.6–1.9 in 72 plant biomass samples collected across paddocks and patch types at peak standing crop, unpublished data). We expected N fractions to show strong demand-driven dynamics which would require frequent measurements over extended periods. On the other hand, long-term nutrient transfer through grazing animals will lead to a build-up of the non-limiting nutrients P and K, making them suitable indicators for this process (Aarons, Gourley, & Hannah, 2015; Schnyder, Locher, & Auerswald, 2010). Per plot, we took a mixed sample of 14 topsoil samples (0–10 cm) using a soil auger of 15 mm diameter. We air-dried samples and analysed them for calcium-acetate-lactate-extractable P and K (Hoffmann, 1991).

TABLE 1 Comparison of (generalised) linear mixed effects models containing single and interactive effects of grazing intensity (GI) and patch type (PT) to explain vegetation and soil parameters, compared to null models containing only block as a fixed effect

		Plot scale					**Patch scale**				
Candidate model		**species richness**	**Simpson diversity**	**Simpson evenness**	**Soil K**	**Soil P**	**species richness**	**Simpson diversity**	**Simpson evenness**	**Soil K**	**Soil P**
Model ΔAIC_c											
GI × PT		8.28	11.02	11.55	8.26	5.75	28.21	30.38	31.30	31.43	21.87
GI + PT		3.39	2.19	4.22	**0.00**	2.24	9.72	7.70	8.51	0.61	6.61
GI		21.07	43.28	10.26	38.44	14.62	5.07	17.83	11.80	21.84	12.66
PT		**0.00**	**0.00**	**0.00**	3.75	**0.00**	3.23	**0.00**	**0.00**	**0.00**	**0.00**
Null		17.82	41.15	6.19	42.37	12.53	**0.00**	11.29	4.90	24.35	7.71
Model w_i											
GI × PT		0.013	0.003	0.003	0.014	0.041	0.000	0.000	0.000	0.000	0.000
GI + PT		0.153	0.250	0.103	**0.855**	0.236	0.006	0.021	0.013	0.424	0.035
GI		0.000	0.000	0.005	0.000	0.000	0.062	0.000	0.002	0.000	0.002
PT		**0.834**	**0.747**	**0.851**	0.131	**0.722**	0.154	**0.976**	**0.906**	**0.576**	**0.944**
Null		0.000	0.000	0.038	0.000	0.001	**0.778**	0.003	0.078	0.000	0.020
R^2											
highest w_i	$R_{(m)}^2$	0.103	0.257	0.071	0.270	0.078	–	0.475	0.360	0.286	0.212
	$R_{(c)}^2$	0.391	0.374	0.159	0.480	0.441	0.451	0.530	0.414	0.866	0.759

Note: The difference between the model AICc and the minimum AICc in the model set (ΔAICc) was used to calculate the model weight w_i, which indicates the probability that the model is the best fitting in the candidate set (model with highest probability in bold).
$R_{(m)}^2$: marginal coefficient of determination—variance explained by GI, PT and their interaction; $R_{(c)}^2$: conditional coefficient of determination—variance explained by all fixed and random effects, both calculated using the "r.squaredGLMM" function of the "MuMIn" package (Lefcheck, 2015).

2.5 | Data analysis

We used the R 3.3.2 software environment (R Core Team, 2016), for four types of data analysis: (a) multi-model inference from (generalised) linear mixed effects models, (G)LMM, to test the effect of experimental design (grazing intensity treatment, patch type) on soil and plant diversity measures at plot and patch scale; (b) structural equation models (*SEM*) to distinguish direct effects of experimental design on plant diversity measures from effects mediated by soil nutrients; (c) nonlinear MANOVA to test the effect of experimental design and soil parameters on vegetation composition at plot and patch scale; (d) linear models to test the effect of grazing intensity treatment and patch-type proportions on plant diversity measures at paddock scale.

2.5.1 | Soil nutrients and diversity measures at plot and patch scale

For the first analysis, we fitted global mixed effects models with the interactive effects of grazing intensity and patch type as fixed effects. Poisson GLMM were chosen to model species richness, and LMM to model Simpson diversity and evenness as well as soil parameters, using the packages "lme4" (Bates, Maechler, Bolker, & Walker, 2015) and "nlme" (Pinheiro, Bates, DebRoy, & Sarkar, 2016). To account for the experimental design, we added block as a fixed effect. We included triplet and paddock as random effects in analyses at plot scale and paddock only in analyses at patch scale (see Appendix S1.1 in Supporting Information for model formulas). Based on these global models, we used multi-model inference to assess evidence for each of the nested models: We ranked these models based on the second-order Akaike Information Criterion (AIC_c) and calculated model weights from each model's ΔAIC_c, that is, the difference of the model's AIC_c to the lowest AIC_c in the candidate model set (Burnham & Anderson, 2002). We then used model averaging on the basis of w_i, implemented in the package "MuMIn" (Barton, 2016), to estimate mean values and confidence intervals.

We analysed total beta diversity and its components analogously, and report mean values and confidence intervals of the model with the lowest AIC_c. We graphically checked all models for normality and homoscedasticity of residuals and addressed violations of the latter by fitting appropriate variance structures. To ensure normality of residuals, we log-transformed Simpson diversity and soil nutrients and logit-transformed beta diversity measures.

2.5.2 | Soil-mediated patch-type and grazing-intensity effects on plant diversity measures

In the second analysis, we tested whether soil nutrients mediated the effects of our experimental design on diversity measures at the plot scale using *SEM*. For this, we used models from the first analysis step for the pathways between experimental design and either soil nutrient concentrations or diversity measures, but added pathways connecting concentrations of soil P and K as additional causal variables for the diversity measures (see Appendix S1.2 for model formulas). To derive confidence intervals for the soil–nutrient–mediated effects of patch type and grazing intensity, we used the R package "RMediation" (Tofighi & MacKinnon, 2011).

2.5.3 | Plant species composition at plot and patch scale

In the third analysis, we addressed species composition as a multivariate dependent variable. At both plot and patch scale, we calculated distance matrices based on Bray Curtis dissimilarity of square-root transformed species abundance data. We performed nonlinear MANOVA implemented in the "adonis" function of the "vegan" package (Oksanen et al., 2017) on these distance matrices. Using marginal sums of squares, we calculated the proportion of variance explained by our explanatory variables after controlling for the block effect. We determined the unique and joined marginal effects of our experimental factors (grazing intensity, patch type and their interaction) as well as the unique and joined marginal effects of soil K and P concentrations. We calculated the shared effect of experimental factors and soil nutrients by subtracting their marginal effects from the total explained variance.

2.5.4 | Plant diversity measures at paddock scale

In the fourth analysis, we predicted paddock-scale diversity from resampled data. Species richness and Simpson diversity were log-transformed before analysis. We used linear models including the interactive effects of the proportion of plots sampled from short patches, both as a linear and as a quadratic term, with grazing intensity as well as a block effect (see Appendix S1.3 for model formulas). From these global models, we chose the models with the lowest AIC_c as the final models (see Table S2).

3 | RESULTS

3.1 | Evidence for patch-type and grazing-intensity effects on plant diversity and soil parameters

Multi-model inference revealed patch type as more important driver of plant diversity and soil P concentrations at the plot scale than grazing intensity: models containing only patch type as a fixed effect had model weights >0.75. For soil K we found evidence for an additional grazing-intensity effect (Table 1). Across grazing intensities, plant diversity was higher (species richness by 37%, Simpson diversity by 92% and Simpson evenness by 27%, Figure 2a–c) and soil nutrient concentration was lower (K by 50%, P by 35%, Figure 2g,h) in short compared to tall patches. At the patch scale, these differences were even more pronounced for Simpson diversity and evenness, whereas for species richness, the null model had the highest model weight (Table 1, Figure 2d,f), indicating that changes in diversity were being driven by changes in evenness rather than species richness at the patch scale. The explanatory power of the fixed effects generally was higher at patch scale (marginal coefficients of determination ($R_{(m)}{}^2$) 0.212–0.475) than at plot scale ($R_{(m)}{}^2$ 0.071–0.103).

3.2 | Direct and soil-mediated patch-type effects on plant diversity

Structural equation models showed that plant diversity measures were most strongly affected by the direct effect of patch type (Figure 3; see also Appendix S1.2). The indirect pathways, mediated through patch-type or grazing-intensity effects on soil nutrient concentrations, were of smaller magnitude (Figure 3b, d, f). The direction of soil-nutrient-concentration effects on plant diversity differed both between the two nutrients and the diversity parameter considered: Species richness increased with decreasing K and increasing P concentrations, while Simpson evenness and soil K were positively related (Figure 3a, c, e). This affected the direction of the soil-mediated effects of patch type and grazing intensity, of which the K-mediated effect was generally stronger than the P-mediated one: K-mediated patch-type effects supported direct patch-type effects on species number, but partly offset direct patch-type effect on Simpson evenness (Figure 3b, d, f). That opposing effects of soil K and P were not an artefact of multicollinearity is borne out by the facts that variance inflation factors in models containing both nutrients remained well below 3 (Appendix S1.2), and that the direction of each nutrient's effect did not change when the other was removed from the model.

3.3 | Vegetation composition

Grazing intensity, patch type and soil nutrients together explained 19.3% and 48.0% of total dissimilarity in plant species composition at the plot and patch scales, respectively (Table 2). Soil nutrients contributed about one third of this explanatory power at plot scale and one quarter at patch scale, with a considerable proportion shared between the two nutrients. At both plot and patch scale, patch type alone contributed more than one third to the explained variation (Table 2). Grazing intensity, together with its interaction with patch type, had a similar explanatory power. Variation shared between grazing intensity and patch type on the one hand and soil nutrients, on the other hand, was very small at both scales.

3.4 | Beta-diversity within and between patch types

Beta-diversity within and between patch types was dominated by species turnover, with relatively small contribution of the nestedness component (Figure 4, Figure S1). At the plot scale, multiple-site dissimilarities within patch types were not affected by grazing intensity or by patch type (Table S1). Null models estimated total dissimilarity as 0.70 (0.68–0.72), species turnover as 0.62 (0.59–0.64) and nestedness as 0.09 (0.08–0.11), with values in brackets representing the 95% confidence intervals.

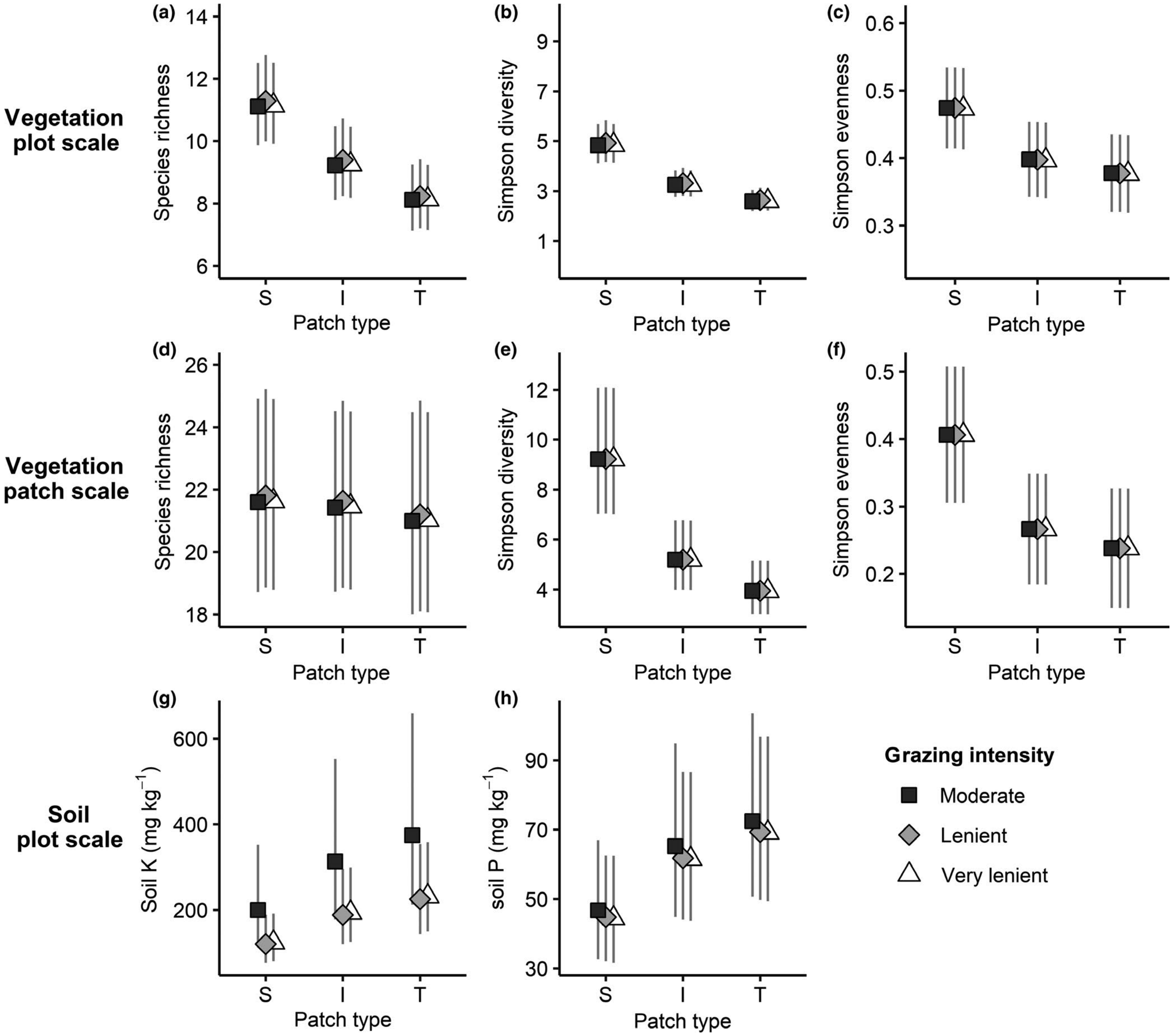

FIGURE 2 Effect of grazing intensity and patch types (S: short, I: intermediate, T: tall) on plant diversity measures at plot (a-c) and patch scale (d-f) and on soil nutrients at plot scale (g-h). Means and confidence intervals estimated through weighted averaging of five candidate (generalised) linear mixed effects models with model probability w_i as a weighting factor (see Table 1)

At the patch scale, there was some evidence that pairwise dissimilarity differed between patch types (model weights for the model containing patch-type pair as fixed effect were 0.57 for species turnover, 0.39 for nestedness and 0.13 for total dissimilarity (Table S1); estimates of these models shown in Figure 4). Species turnover was higher between short and tall than between intermediate and tall patches. For nestedness and total dissimilarity, however, the null model had the greatest probability (model weights of 0.56 and 0.80, respectively).

3.5 | Paddock-scale diversity

When plot-scale data were resampled to represent different proportions of short and tall patches, both Simpson diversity and Simpson evenness increased linearly with increasing proportion of short patches, without influence of grazing intensity (Figure 5, Table S2). Between the short:tall-patch ratio representative of the very lenient (0.28:1) and moderate (3.75:1) grazing intensities, Simpson diversity increased from 2.96 to 4.27 and Simpson evenness from 0.13 to 0.17, albeit with considerable variation between paddocks (Figure 5b, c). The most probable model for species richness included the interaction between grazing intensity and proportion of short patches: the increase in species richness with increasing proportion of short patches was strongest in the moderate grazing intensity, while confidence intervals for this slope covered zero in the lenient and very lenient grazing intensity. Variation between paddocks was high, and estimates at the representative short:tall-patch ratios for the three grazing intensities did not significantly differ from each other (Figure 5a).

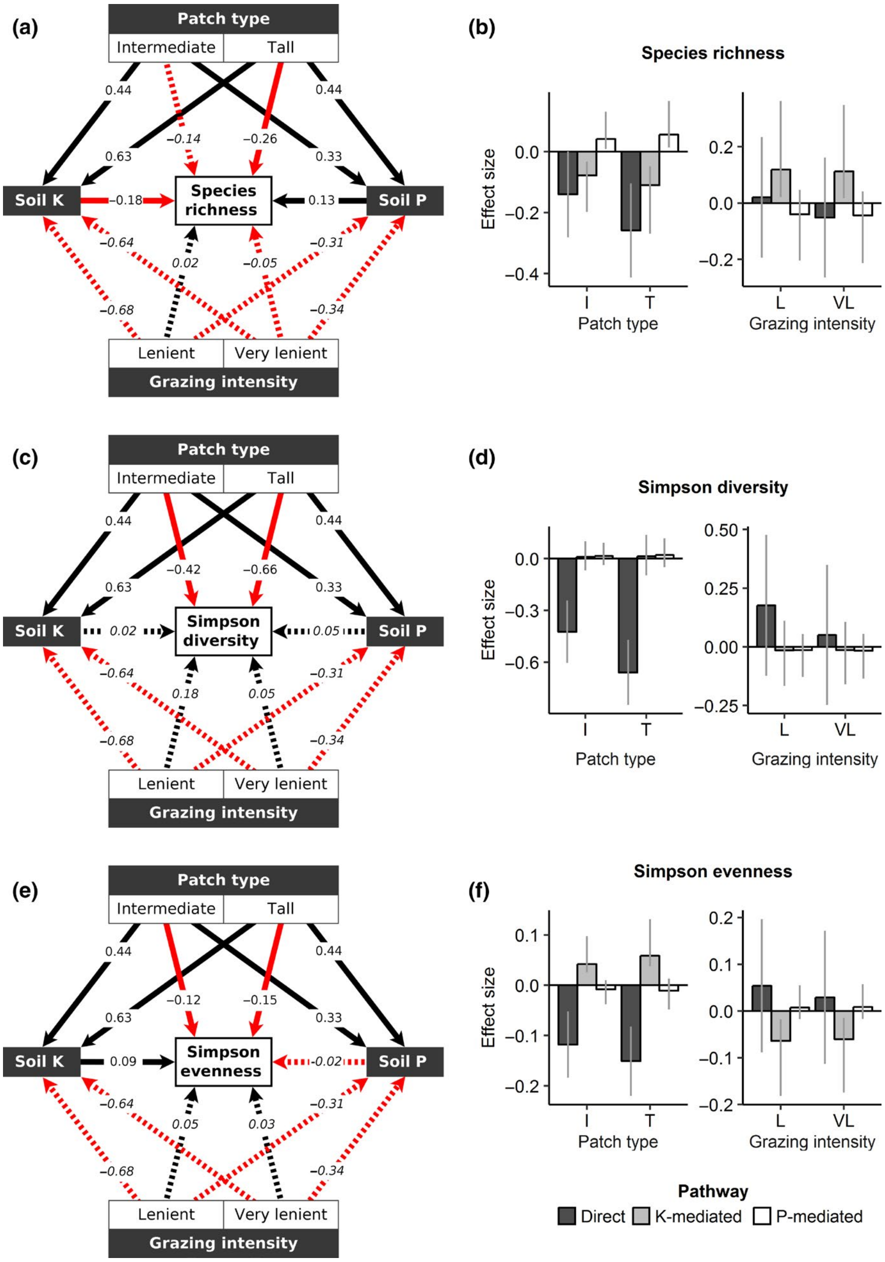

FIGURE 3 (a, c, e): Piecewise structural equation models of the direct and soil-nutrient-mediated effects of grazing intensity and patch type on plant diversity measures: species richness (a, log scale), Simpson diversity (b, log scale), Simpson evenness (c); soil K and soil P: log-scale, measurement unit: mg kg^{-1}. Black arrows denote positive relationships, red arrows negative ones; numbers along arrows are unstandardised path coefficients. These coefficients can be interpreted as partial regression coefficients. Where their confidence intervals cover zero this is indicated by a dashed line and figures in italics. The categorical variables grazing intensity and patch type are coded by dummy variables relative to a reference level. For grazing intensity, this reference level is “moderate grazing”, for patch type it is “short patch”. Block effects (not shown; see Appendix S1.2) on species richness, soil K and soil P were included in all candidate models. (b, d, f): Total direct and soil-nutrient (P, K) mediated effects of patch type (I: intermediate, T: tall) and grazing intensity (L: lenient, VL: very lenient) on plant diversity measures, derived from the unstandardised path coefficients of the structural equation models; error bars: 95% confidence intervals

4 | DISCUSSION

4.1 | Patch-type effects on plant diversity and composition

As hypothesised (H1, H2; Figure 1), plant diversity at both plot and patch scale was more strongly driven by patch type than by paddock-scale grazing intensity (Table 1): Short patches had higher Simpson diversity and evenness than tall patches, and higher species richness at the plot scale (Figure 2). Higher species richness or evenness in frequently grazed short compared to rarely grazed tall patches has been reported from several mesic grazing systems (Bakker et al., 1983; Knapp et al., 1999; Marion et al., 2010; Posse, Anchorena, & Collantes, 2000).

In contrast to our expectation (H2, Figure 1), we found no evidence that patch-type effects on plant diversity measures were primarily mediated by soil nutrient concentration (Figure 3), or that soil nutrient concentration explained species composition jointly with patch type (Table 2). This makes biomass removal through grazing the most likely driver of patch-type differences in plant diversity: Frequent defoliation maintains short patches at low levels of standing biomass, reducing light limitation compared to tall patches. Decreased light limitation, in turn, has been identified as a mechanism by which herbivores increase plant species richness (Borer et al., 2014). A recent global study suggests that herbivores decrease light limitation by reducing the abundance of dominant species (Koerner et al., 2018). This corresponds with our observation that

TABLE 2 Variance partitioning based on nonlinear MANOVA on Bray–Curtis distances of plant species abundances at plot (n = 135) and patch scale (n = 27)

	Scale	
Cause of variation	**Plot**	**Patch**
experimental factors	*0.130 (0.676)*	*0.353 (0.737)*
grazing intensity (GI)	0.038 (0.198)	0.106 (0.222)
patch type (PT)	0.073 (0.376)	0.176 (0.367)
GI × PT	0.020 (0.102)	0.071 (0.148)
soil	*0.068 (0.354)*	*0.127 (0.265)*
K	0.051 (0.262)	0.081 (0.169)
P	0.043 (0.223)	0.082 (0.170)
experimental factors/soil shared	*0.006 (0.030)*	*0.001 (0.002)*

Note: Variance explained by experimental factors (grazing intensity, patch type and their interaction) and soil nutrients after controlling for block effects, based on marginal sums of squares. In brackets: values in relation to the total proportion of variance explained by experimental factors and soil variables together (plot-scale: 0.193, patch scale: 0.480). Rows in italics refer to variance explained jointly by groups of variables (experimental factors, soil) or shared between these groups.

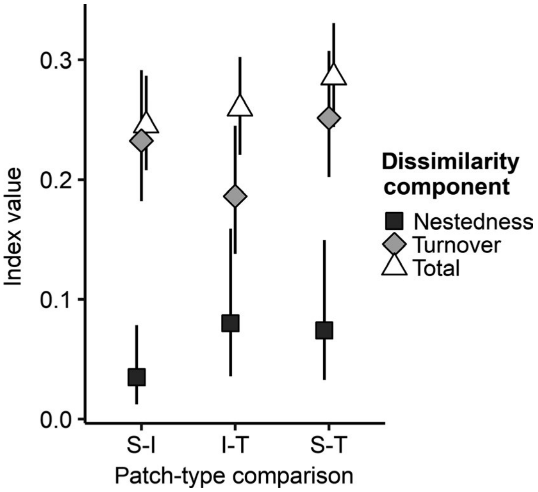

FIGURE 4 Pairwise dissimilarity in vegetation composition between patch types: short (S), intermediate (I) and tall (T). Estimates and 95% confidence intervals of linear mixed effects models for total dissimilarity (Soerensen dissimilarity) and its species turnover (Simpson dissimilarity) and nestedness components

evenness responded even more strongly to patch type than species richness (Figure 2a, c, d, f), a reaction that appears to be common in grasslands grazed by large herbivores (Jia et al., 2018).

While we did not observe strong soil nutrient effects on plant diversity parameters, it has to be noted that the soil K gradient between individual plots within patch types (varying by a factor of 16 to 21, n = 27) was much smaller than the gradient between individual plots across patch types (varying by a factor of 34, n = 135). Further studies could elucidate whether this represented the full gradient existing within each patch type, and whether effect of soil nutrients on diversity might be clearer when the sampled gradients are extended to their full length.

Patch types differed not only in species richness, but also in the identity of the species that were present in each (Table 2, Figure 4). Based on the Simpson dissimilarities (Figure 4), we calculated species turnover to equal 0.22–0.34 of the species number shared between each of two patch types. Species turnover was highest between tall and short and lowest between tall and intermediate patches. Overall, however, the contribution of intermediate and tall patches to beta diversity was not sufficient to offset their lower diversity at plot scale when paddock-scale diversity measures were calculated (Figure 5). In consequence, paddock-scale diversity measures were highest at the highest proportion of short patches and not when contributions of short and tall patches were equal.

4.2 | Grazing-intensity effects on plant diversity and composition

In contrast to patch type, grazing intensity, alone or in interaction with patch type, only affected plant composition, not plant diversity. This extends earlier results from our experiment that failed to find effects of paddock-scale grazing intensity on plant diversity in randomly located permanent plots (Wrage, Şahin Demirbağ, Hofmann, & Isselstein, 2012). It is also in line with a study reporting interactive effects of grazing intensity and patch type on botanical composition in another long-term grazing experiment (Ludvíková et al., 2015).

The grazing-intensity effects on vegetation composition that we observed were largely independent from soil nutrient effects (Table 2). They are also unlikely to derive from a difference in defoliation intensity, as this varied predominantly between patch types. Intensity of both animal-mediated seed dispersal and trampling, however, are related to animal density at paddock scale. Endo- and epizoochoric seed dispersal through ungulates can act as ecological filters and therefore affect species composition (Albert et al., 2015). At the same time, the relationship between dispersal rates and local plant diversity is not straightforward (Cadotte, 2006). Similarly, trampling, experimentally separated from other grazing influences, has been shown to influence botanical composition without affecting plant diversity (Lezama & Paruelo, 2016). This may explain why we found plot- and patch-scale effects of grazing intensity on vegetation composition (Table 2) but not diversity (Table 1, Figure 2).

4.3 | Patterns of soil nutrient concentration

Soil K and P differed far more strongly between patch types than between grazing intensities (Table 1, Figure 2). As we expected (H2, Figure 1), available soil K and P concentrations were lower under short than under tall patches. In this, our results differed from those obtained in other patch-grazing systems, where the opposite was found (Augustine, McNaughton, & Frank, 2003; Güsewell, Jewell, & Edwards, 2005). Higher nutrient concentrations in preferentially

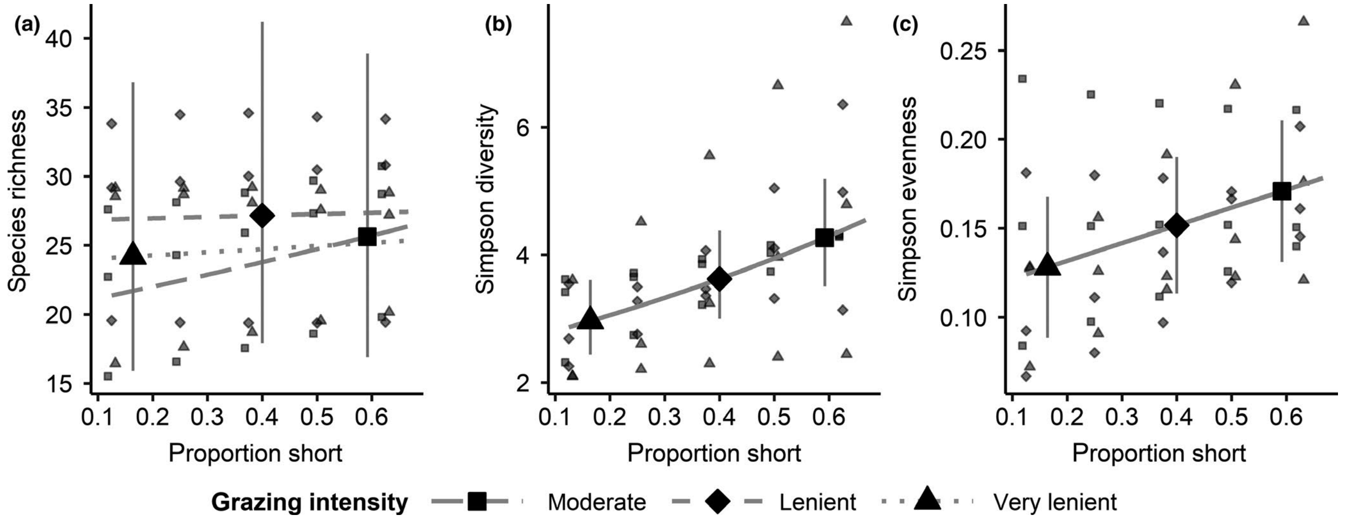

FIGURE 5 Paddock-scale species richness (a), Simpson diversity (b) and Simpson evenness (c) as affected by the distribution of patch types (proportion of short patches) and paddock-scale grazing intensity. Paddock-scale diversity measures result from plot data resampled within each paddock so as to vary the proportion of short and tall patches between 0.125 and 0.625, with the proportion of intermediate patches constant at 0.25. Small symbols: mean values for individual paddocks, line: model predictions, large symbols: model predictions at the mean proportion of short versus tall patches actually observed for the three grazing intensities, error bars: 95% confidence intervals

grazed compared to rarely grazed patches can be expected when a higher soil nutrient status improves biomass forage nutritive value to a degree that this becomes the driver for the grazing pattern (Güsewell et al., 2005; McNaughton, 1988). This seems to be the case in dystrophic habitats, while the reasons for the initial placement of preferred grazing areas in more nutrient-rich areas are complex and not necessarily related to soil characteristics (Hempson et al., 2015; Posse et al., 2000). Net nutrient imports into preferred wet-season grazing areas were found in the Serengeti (Augustine et al., 2003). These occurred during the dry season, when ungulates used these areas as resting places to avoid predation, yet foraged in the surrounding bushland. Preferential grazing can also affect soil nutrient status by reducing nitrogen losses which occur in the case of fire (Knapp et al., 1999). These examples illustrate the complex interplay between animal behaviour, vegetation and environmental conditions in shaping patch-grazing nutrient dynamics. In the majority of European mesotrophic grasslands, however, we expect that these are dominated by a net nutrient transport from short to tall patches through spatial decoupling of grazing and non-grazing behaviour patterns (Schnyder et al., 2010).

We used both soil P and K as indicators for long-term, cattle-mediated nutrient transfer in our study, even though previously determined plant nutrient ratios at peak standing crop indicate that nitrogen is the nutrient limiting plant growth at our site. This is justified as nitrogen and P are jointly redistributed through grazing animals (Güsewell et al., 2005; Schnyder et al., 2010). While K was not considered in the two cited studies, it is more mobile than P (Whitehead, 2000) and may even better reflect animal-mediated nutrient dynamics since the start of the experiment. By contrast, directly measuring nitrogen availability to plants in grasslands is difficult, as pointed out in a recent study by Mládková et al. (2015): After 7 to 8 years of differentiated management, only extractable soil P and K, but neither soil total nitrogen nor the ratio between soil organic carbon and soil total nitrogen differed between mown, grazed and fallow plots. Extractable soil P also best explained plant productivity under grazing, even though nutrient indices suggested that nutrient deficiency was strongest for nitrogen (Mládková et al., 2015). These results support or use of K and P as indicators of nutrient transfer by cattle.

4.4 | Paddock-scale plant diversity

As hypothesised (H3, Figure 1), the relative proportions of short and tall patches, which result from different paddock-scale grazing intensities, were the main driver for paddock-scale diversity. This relationship was significant for Simpson diversity and Simpson evenness in spite of considerable variation between paddocks (Figure 5). Against our expectations (H4, Figure 1), however, diversity measures did not reach their maximum at the most even distribution of height classes but increased linearly with the proportion of short patches (Figure 5). This result is surprising, as the proportion of short patches is maximised under high grazing intensities, for which theory predicts low plant diversity (Cingolani et al., 2005; Milchunas et al., 1988).

Our failure to find evidence for such a relationship could be caused by an insufficiently long gradient in grazing intensity. Increasing stocking rates beyond those applied in our moderate grazing treatment, however, would require either fertiliser application or a change from continuous to rotational stocking (Lemaire, Silva, Agnusdei, Wade, & Hodgson, 2009). Fertiliser application would simultaneously increase resource availability and permit more frequent defoliation due to increased plant growth rates (Lemaire et al., 2009), thus substantially changing the growing conditions in short patches. Rotational stocking involves high stocking rates over short periods and decreases grazing selectivity. The proportion of the area that remains ungrazed in each rotation can be as low as 5%–15%, consisting mostly of rejected dung and urine patches (Tuñon et al., 2014). By contrast, in our experiment intermediate and tall patches still covered 25% and 16% of the paddocks even under moderate grazing. Although tall patches apparently did not substantially contribute to plot-scale (Figure 2a-c), patch-scale (Figure 2d-f) or paddock-scale (Figure 5) diversity, we cannot rule out that they play an important role in maintaining the high diversity of short patches. Besides acting as sink for the nutrients exported from the short patches (Figure 2g, h), they may serve as a forage buffer during periods of low regrowth: Typically, some proportion of tall patches is grazed more intensely at the end of the grazing season (Rossignol et al., 2011). This may prevent overgrazing and permit generative reproduction in short patches. Consequently, our results should not be generalised beyond continuously stocked, unfertilised pastures.

Organism groups also differ in their reactions to grassland vegetation heterogeneity. In our experiment, higher diversity and abundances of grasshoppers and butterflies were found under lenient and very lenient than under moderate grazing (Jerrentrup, Wrage-Mönnig, Röver, & Isselstein, 2014). Grazing intensity effects on plant composition show that even among plants, species differed in their reaction to paddock-scale grazing intensity, and further research should look into functional attributes of the plant species that are promoted under more lenient grazing.

5 | CONCLUSIONS

Our study clearly revealed the grazing-induced patch structure was a more important driver of plant diversity than paddock-scale grazing intensity. Management strategies and evaluation criteria that do not explicitly consider this patch structure may fail to either achieve or detect biodiversity benefits in extensive grazing systems. The high plant diversity found in short patches points towards larger possible synergies between biodiversity conservation and agronomic production under low-intensity grazing than commonly assumed: in a management system without external nutrient input, plant diversity may peak at comparatively high stocking rates, when management promotes structural heterogeneity of the pasture.

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AUTHORS' CONTRIBUTIONS

B.T. and J.I. conceived and designed the study; E.M.D. and J.G. collected the data; B.T., E.M.D. and J.G. analysed the data; B.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data are available via the Zenodo data repository http://doi.org/10.5281/zenodo.2657634 (Tonn, Densing, Gabler, & Isselstein, 2019).

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SUPPORTING INFORMATION

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

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Supplorting information for the paper

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Grazing-induced patchiness, not grazing intensity, drives plant diversity in European low-input pastures

Journal of Applied Ecology

Appendix S1 Details on the data analyses

Figure S1. Dissimilarity in vegetation composition within and between patch types; raw data and means per treatment and grazing intensity

Table S1. Comparison of linear mixed effects models explaining plant diversity measures as response to grazing intensity and patch type or patch-type comparison

Table S2. Comparison of linear mixed effects models explaining paddock-scale diversity parameters as response to grazing intensity and proportion of short patches within a paddock

Figure S2 Effect of number of plots sampled on diversity parameters

Appendix S1. Details on the data analyses.

The appendix provides additional information for three of the four data analysis steps described in sections 2.5.1, 2.5.2 and 2.5.4 of the paper. Formulae of the (generalized) linear mixed effects models follow the syntax of the R 3.3.2 software environment (R Core Team, 2016) statistical packages that were used to fit the models: 'lme4' (Bates et al., 2015) for generalized linear mixed effects models, 'nlme' (Pinheiro et al., 2016) for linear mixed effects models.

Table 1 Appendix S1. List of abbreviated model terms.

Abbreviation	**Explanation**
`pt`	patch type; factor levels 'short' (reference level), 'intermediate' (`ptI`), 'tall' (`ptT`)
`ptc`	patch type comparison for between-patch-type beta diversity; factor levels 'short-intermediate', 'intermediate-tall', 'short-tall'
`gi`	paddock-scale grazing intensity; factor levels 'moderate' (reference level), 'lenient' (gi2), 'very lenient' (gi3)
`block`	experimental block; factor levels 'A' (reference level), 'B', (`blockB`), 'C' (`blockC`),
`paddock`	experimental paddock; three paddocks per grazing-intensity treatment
`triplet`	five triplets, containing one plot of each patch type, per paddock
`log_p`	log-transformed concentrations (mg kg^{-1}) of CAL-extractable soil phosphorus
`log_k`	log-transformed concentrations (mg kg^{-1}) of CAL-extractable soil potassium
`sr`	species richness
`log_d`	log-transformed Simpson diversity
`e`	Simpson evenness
`logit_sor`	logit-transformed Soerensen dissimilarity (total *β* diversity)
`logit_sim`	logit-transformed Simpson dissimilarity (species turnover)
`logit_sne`	logit-transformed nestedness component of *β* diversity
`prop_short`	proportion of plots sampled from short patches out of an eight-plot sample to calculate paddock-scale diversity; unique values: 0.125, 0.25, 0.375, 0.5, 0.625
`prop_short_sq`	square of `prop_short`

Appendix S1.1 Soil nutrients and diversity measures at plot and patch scale

As part of the first analysis (section 2.5.1 of the journal article), we assessed the interactive effects of grazing intensity and patch type on species richness, Simpson diversity, Simpson evenness, soil K concentration and soil P concentration at plot and patch scale. To account for the experimental design, we added block as a fixed effect. We included triplet and paddock as random effects in analyses at plot scale and paddock only in analyses at patch scale. The results of this analysis are presented in Table 1 and Figure 2.

We fitted the following global models to data at the plot scale (n = 135):

```
M_plot_sr <- glmer(sr ~ gi * pt + block + (1 | paddock) + (1 | triplet),
             family = poisson)

M_plot_d <- lme(log_d ~ gi * pt + block, random = ~ 1 |paddock/triplet)

M_plot_e <- lme(e ~ gi * pt + block, random = ~ 1 | paddock / triplet)

M_plot_k <- lme(log_k ~ gi * pt + block, random = ~ 1 | paddock / triplet,
            weights = varIdent(form = ~ 1 | gi))

M_plot_p <- lme(log_p ~ gi * pt + block, random = ~ 1 | paddock / triplet)
```

We fitted the following global models to data aggregated at the patch scale (n = 27):

```
M_patch_sr <- glmer(sr ~ gi * pt + block + (1 | paddock), family = poisson)

M_patch_d <- lme(log_d ~ gi * pt + block, random = ~ 1 | paddock)

M_patch_e <- lme(e ~ gi * pt + block, random = ~ 1 |paddock)

M_patch_k <- lme(log_k ~ gi * pt + block, random = ~ 1 | paddock,
             weights = varIdent(form = ~ 1 | gi))

M_patch_p <- lme(log_p ~ gi * pt + block, random = ~ 1 | paddock)
```

We analogously analysed beta diversity parameters (total dissimilarity and its nestedness and turnover components) at plot scale and patch scale; the results are presented in Fig. 5 and Table S1. At the plot scale, we analysed *β* diversity within each patch type. At the patch scale, we analysed pairwise *β* diversity between patch types. In the models, 'patch type' is replaced by 'patch type comparison', i.e. the respective pairs of patch types.

We fitted the following global models to data at the plot scale (n = 135):

```
M_sor_plot <- lme(logit_sor  ~ pt * gi + block,
                  random = ~ 1 | paddock,
                  weights = varIdent(form = ~ 1 | pt))

M_sim_plot <- lme(logit_sim  ~ pt * gi + block,
                  random = ~ 1 | paddock,
                  weights = varIdent(form = ~ 1 | pt))

M_sne_plot <- lme(logit_sne  ~ pt * gi + block,
                  random = ~ 1 | paddock)
```

We fitted the following global models to data aggregated at the patch scale (n = 27):

```
M_sor_patch <- lme(logit_sor  ~ ptc * gi + block,
                   random = ~ 1 | paddock)

M_sim_patch <- lme(logit_sim  ~ ptc * gi + block,
                   random = ~ 1 | paddock,
                   weights = varExp(form = ~ logit_sim))

M_sne_patch <- lme(logit_sne  ~ ptc * gi + block,
                   random = ~ 1 | paddock)
```

Appendix S1.2 Soil-mediated patch-type and grazing-intensity effects on diversity parameters

The second analysis (section 2.5.2 of the journal article), used piecewise structural equation models (SEM) implemented in the R 3.3.2 package 'piecewiseSEM' (Lefchek, 2015). We based the component models for the piecewise SEM on models from the first analysis step. We modelled soil parameters using linear mixed effects models containing patch type, grazing intensity and block as fixed effects (best candidate model for soil K, second best candidate model for soil P, Table 1):

```
M_sem_p <- lme(log_p ~ pt + gi + block,
               random = ~ 1 | paddock / triplet)

M_sem_k <- lme(log_k ~ pt + gi + block,
               random = ~ 1 | paddock / triplet,
               weights = varIdent(form = ~ 1 | gi)
```

Diversity parameters were modelled using (generalized) linear mixed effects models containing patch type, grazing intensity, soil P, soil K and block as fixed effects. We included grazing intensity even though it was not present in the respective best models (Table 1), as accounting for the soil-mediated patch-type effect on diversity parameters might reveal an additional direct effect of grazing intensity:

```
M_sem_sr <- glmer(sr ~ pt + gi + k + p + block +
                  (1 | paddock) + (1 | triplet),
                  control = glmerControl(optimizer = "bobyqa",
                                         optCtrl = list(maxfun=2e5)),
                  family = poisson)

M_sem_e <- lme(e ~ pt + gi + k + p + block,
               random = ~ 1 | paddock / triplet)

M_sem_d <- lme(log_d ~ pt + gi + k + p + block,
               random = ~ 1 | paddock / triplet)
```

To assess the degree of collinearity between independent variables in these models, we determined variance inflation factors for the generalized linear mixed effects models, using the 'vif.mer' function (Frank, 2014), and generalized variance inflation factors for the linear mixed effects models, using the 'vif' function of the 'car' package (Fox & Weisberg, 2011). We present these in Table 2 Appendix S1, together with the models' marginal coefficient of determination ($R_{(m)}^2$, variance explained by fixed effects other than block) and conditional coefficient of determination ($R_{(c)}^2$, variance explained by all fixed and random effects).

Fig. 3 presents path coefficients of the resulting piecewise SEMs. Table 3 Appendix S1 additionally contains the standard errors of these path coefficients, as well as the path coefficients of the experimental blocks, which are omitted from Fig. 3 for greater clarity.

We used the unstandardized path coefficients of the piecewise structural equation models to separately calculate the effect sizes of soil-K-mediated, soil-P-mediated and total patch-type and grazing-intensity effects on diversity parameters (Fig. 4). The effect sizes of the soil-mediated effects are the product of the path coefficients along the compound path. For example, the soil-K-mediated effect of tall compared to short patch on species richness equals the path coefficient between tall patch and soil K (0.63) multiplied with path coefficient between soil K and species richness (-0.11), resulting in an effect size of 0.11. The higher soil K concentration of tall compared to short patches causes species richness to decrease. As species richness is analysed on the log-scale, the effect size of

-0.11 translates into an 10% decrease of species richness in short compared to tall patches ($e^{-0.11}$ = 0.90, i.e. Species richness of tall patches is 90% that of tall patches), which is mediated by the increased soil K concentration of tall patches. We derived confidence intervals for the effect sizes of these compound paths using the package 'RMediation' (Tofighi & MacKinnon, 2011).

Table 2 Appendix S1. Variance inflation factors for all terms contained in the component models of the structural equation models, as well as marginal ($R_{(m)}^2$) and conditional ($R_{(c)}^2$) coefficients of variation of these component models.

model	model terms	variance inflation factors	$R_{(m)}^2$	$R_{(c)}^2$
`M_sem_sr`	`ptI`	1.50	0.269	0.396
	`ptT`	1.68		
	`gi2`	1.58		
	`gi3`	1.54		
	`log_k`	2.18		
	`log_p`	1.61		
	`block`B	1.40		
	`block`C	1.41		
`M_sem_e`	`pt`	1.27	0.139	0.324
	`gi`	1.07		
	`log_k`	1.99		
	`log_p`	1.67		
	`block`	1.00		
`M_sem_d`	`pt`	1.26	0.338	0.413
	`gi`	1.12		
	`log_k`	2.09		
	`log_p`	1.72		
	`block`	1.00		

Table 3 Appendix S1. Unstandardised path coefficients (estimates and standard errors) of the structural equation models. For abbreviations of response and predictor variables see Table 1 Appendix S1.

response variable	predictor variable	path coefficient	
		estimate	standard error
log_k	blockB	0.04086	0.30222
log_k	blockC	-0.02891	0.30222
log_k	ptI	0.44642	0.08723
log_k	ptT	0.62617	0.08723
log_k	gi2	-0.68028	0.30547
log_k	gi3	-0.64203	0.30391
log_p	blockB	-0.06354	0.34624
log_p	blockC	-0.13877	0.34624
log_p	ptI	0.32734	0.10675
log_p	ptT	0.43963	0.10675
log_p	gi2	-0.31333	0.34624
log_p	gi3	-0.34596	0.34624
sr	blockB	0.31930	0.10247
sr	blockC	0.29892	0.10282
sr	ptI	-0.14001	0.07189
sr	ptT	-0.25830	0.07893
sr	gi2	0.02031	0.10947
sr	gi3	-0.05118	0.10888
sr	log_k	-0.17516	0.07204
sr	log_p	0.12661	0.06331
e	blockB	0.00248	0.07096
e	blockC	-0.03777	0.07098
e	ptI	-0.11794	0.03359
e	ptT	-0.15090	0.03510
e	gi2	0.05381	0.07284
e	gi3	0.02903	0.07259
e	log_k	0.09391	0.02948
e	log_p	-0.02455	0.02754
log_d	blockB	0.36759	0.14670
log_d	blockC	0.25496	0.14676
log_d	ptI	-0.42315	0.09191
log_d	ptT	-0.65919	0.09593
log_d	gi2	0.17688	0.15330
log_d	gi3	0.05071	0.15242
log_d	log_k	0.02253	0.08041
log_d	log_p	0.04674	0.07499

Appendix S1.3 Diversity parameters at paddock scale

The fourth analysis (section 2.5.4 of the journal article), used a data set derived from all possible combinations of the 15 plots per paddock that resulted in an eight-plot sample consisting of two plots from the intermediate patch type, one to five plots of the tall patch type and five to one plots of the short patch type. The proportion of short patches in the combination sample (`p_short`) therefore was 0.125, 0.25, 0.375, 0.5 or 0.625. For each of these samples, we determined species richness, Simpson diversity and Simpson evenness. We then calculated mean values for each paddock and level of `p_short`. We then fitted models including grazing intensity, `p_short`, the squared value of p_short (`p_short_sq`), and the interactions of grazing intensity with `p_short` and `p_short_sq` with grazing intensity as explanatory models.

We fitted the following models:

```
M_sr_paddock <- lme(log(sr) ~ gi + prop_short + prop_short_sq +
                    gi : prop_short +  gi : prop_short_sq + block,
                    random = ~ 1 | paddock,
                    weights = varIdent(form = ~ 1 | gi))

M_d_paddock <- lme(log_d ~ gi + prop_short + prop_short_sq +
                   gi : prop_short +  gi : prop_short_sq + block,
                   random = ~ 1 | paddock,
                   weights = varIdent(form = ~ 1 | gi))

M_e_paddock <- lme(e ~ gi + prop_short + prop_short_sq +
                   gi : prop_short +  gi : prop_short_sq + block,
                   random = ~ 1 | paddock,
                   weights = varIdent(form = ~ 1 | gi))
```

We show results of the model selection in Table S2, and diversity parameters predicted by the best model in Fig. 5.

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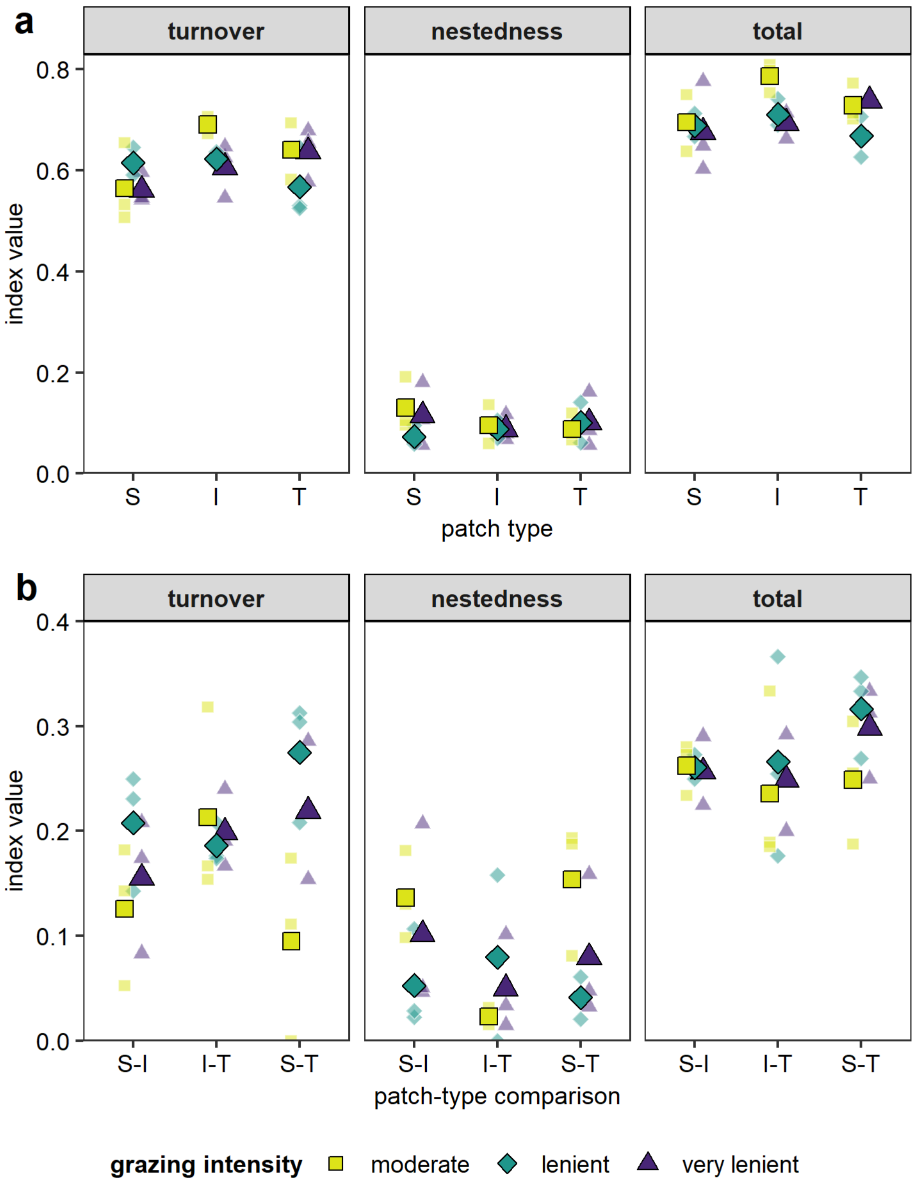

Figure S1. Dissimilarity in vegetation composition within and between patch types: total dissimilarity (Soerensen dissimilarity) and its species turnover (Simpson dissimilarity) and nestedness components. (a) plot scale: multiple-site dissimilarity between five plots of the same patch type (S: short, I: intermediate, T: tall) within each paddock; (b) patch scale: pairwise dissimilarity between two patch types. Small, semi-transparent symbols: paddock values; large symbols: means across paddocks for each grazing intensity. Model estimates of patch-scale beta diversity are shown in Fig. 5.

Table S1. Comparison of linear mixed effects models containing single and interactive effects of grazing intensity (GI) and patch type (PT) or patch-type comparison (PTC) to explain total dissimilarity (Soerensen dissimilarity) and its species turnover (Simpson dissimilarity) and nestedness components at plot and patch scale, compared to null models containing only block as a fixed effect. $R_{(m)}^2$, $R_{(c)}^2$: marginal and conditional coefficient of determination. For further details see Table 1.

	candidate model					
scale of analysis	response variable	fixed effects	ΔAICc	w_i	$R_{(m)}^2$	$R_{(c)}^2$
plot scale	species turnover	GI × PT	30.68	0.000	0.703	0.766
		GI + PT	7.41	0.016	0.610	0.736
		GI	2.64	0.174	0.470	0.652
		PT	2.77	0.162	0.222	0.231
		Null	**0.00**	**0.648**	**0.000**	**0.015**
	nestedness	GI × PT	35.41	0.000	0.173	0.300
		GI + PT	14.03	0.001	0.055	0.183
		GI	5.90	0.048	0.037	0.165
		PT	6.49	0.036	0.018	0.146
		Null	**0.00**	**0.916**	**0.000**	**0.128**
	total dissimilarity	GI × PT	30.58	0.000	0.690	0.684
		GI + PT	9.25	0.007	0.456	0.421
		GI	2.06	0.248	0.246	0.231
		PT	5.23	0.051	0.117	0.144
		Null	**0.00**	**0.694**	**0.000**	**0.028**
patch scale	species turnover	GI × PTC	24.35	0.000	0.002	0.041
		GI + PTC	1.09	0.329	0.000	0.000
		GI	9.92	0.004	0.001	0.003
		PTC	**0.00**	**0.567**	**0.003**	**0.000**
		Null	3.46	0.101	0.000	0.004
	nestedness	GI × PTC	22.29	0.000	0.418	0.696
		GI + PTC	7.58	0.013	0.248	0.445
		GI	5.20	0.041	0.087	0.207
		PTC	0.72	0.389	0.162	0.443
		Null	**0.00**	**0.557**	**0.000**	**0.204**
	total dissimilarity	GI × PTC	33.21	0.000	0.231	0.352
		GI + PTC	10.00	0.005	0.174	0.295
		GI	4.93	0.068	0.068	0.191
		PTC	3.70	0.126	0.106	0.228
		Null	**0.00**	**0.801**	**0.000**	**0.123**

Table S2. Comparison of linear mixed effects models explaining paddock-scale diversity parameters, and containing single and interactive effects of grazing intensity (GI) and proportion of short patches within a paddock, both as a linear (p_s) and as a quadratic term (p_s^2), as well as block, compared to null models containing only block as a fixed effect. Fixed effects included in the respective model are marked by a ‘+’ sign; block was included in all models. The final model used to predict diversity parameters (Fig. 6) is marked in bold. $R_{(m)}^2$, $R_{(c)}^2$: marginal and conditional coefficents of determination. For further details see Table 1.

response variable	**fixed effects**					**ΔAICc**	**w_i**	**$R_{(m)}^2$**	**$R_{(c)}^2$**
	p_s	**p_s^2**	**GI**	**p_s x GI**	**p_s^2 x GI**				
species richness	**+**		**+**	**+**		**0.00**	**0.758**	**0.096**	**0.989**
	+	+	+	+		3.45	0.135	0.097	0.989
		+	+		+	5.10	0.059	0.095	0.985
	+	+	+		+	5.67	0.045	0.095	0.987
	+	+	+	+	+	12.10	0.002	0.097	0.989
	+					13.82	0.001	0.001	0.911
		+				14.91	0.000	0.001	0.909
	+	+				16.41	0.000	0.001	0.911
						18.46	0.000	0.000	0.888
	+		+			19.28	0.000	0.064	0.911
		+	+			20.38	0.000	0.063	0.909
	+	+	+			22.27	0.000	0.064	0.910
			+			23.56	0.000	0.061	0.888
Simpson diversity	**+**					**0.00**	**0.644**	**0.315**	**0.795**
	+	+				2.73	0.165	0.315	0.796
		+				3.29	0.124	0.299	0.775
	+		+			5.57	0.040	0.324	0.795
	+	+	+			8.63	0.009	0.324	0.796
		+	+			8.87	0.008	0.308	0.775
	+		+	+		8.97	0.007	0.337	0.812
	+	+	+	+		12.41	0.001	0.338	0.812
	+	+	+		+	12.64	0.001	0.337	0.811
		+	+		+	12.76	0.001	0.320	0.791
	+	+	+	+	+	20.07	0.000	0.338	0.813
						35.30	0.000	0.000	0.408
			+			40.57	0.000	0.009	0.408
Simpson evenness	**+**					**0.00**	**0.337**	**0.143**	**0.750**
		+				0.01	0.335	0.143	0.750
	+	+				2.58	0.093	0.145	0.752
	+		+	+		2.94	0.077	0.228	0.805
		+	+		+	3.07	0.073	0.227	0.804
	+		+			5.22	0.025	0.184	0.751
		+	+			5.23	0.025	0.184	0.751
	+	+	+	+		6.17	0.015	0.229	0.806
	+	+	+		+	6.28	0.015	0.229	0.806
	+	+	+			8.13	0.006	0.186	0.752
	+	+	+	+	+	13.85	0.000	0.230	0.807
						16.48	0.000	0.000	0.574
			+			21.40	0.000	0.041	0.574

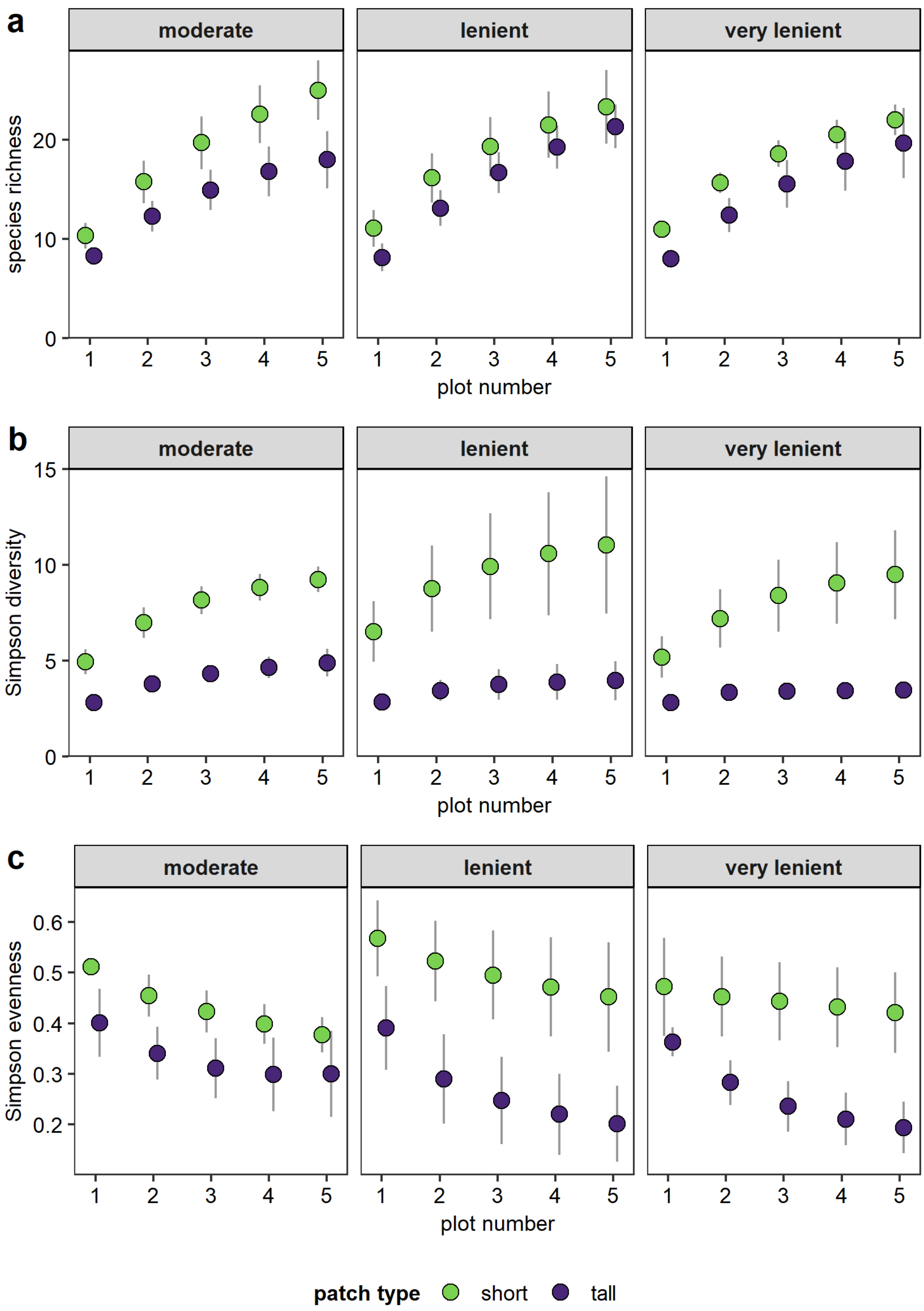

Figure S2. Effect of number of plots sampled on (a) species richness, (b) Simpson diversity and (c) Simpson evenness of short and tall patches under three grazing intensities (moderate, lenient, very lenient). Mean value and standard error for n = 3 paddocks. We sampled all possible combinations of one to five plots out of a total of five investigated plots per paddock and patch type and calculated diversity measures for each of these samples. We calculated mean values for each paddock, patch type and plot number. Symbols are means and error bars standard errors over three blocks.