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RESEARCH ARTICLE

Can we have it all? The role of grassland conservation in supporting forage production and plant diversity

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Abstract
Context A key global challenge is to meet both the growing demand for food and feed while maintaining biodiversity's supporting functions. Protected grasslands, such as Natura 2000 sites in Europe, may play an important role in harmonising productivity and biodiversity goals. This work contributes to an understanding of the relationship between forage production and plant diversity in protected and non-protected grasslands.
Objectives We aimed to identify differences in plant diversity and forage production between protected and non-protected grasslands by assessing the effects of land-use intensity (i.e. mowing, grazing, fertilising) on these variables.
Methods Data were available for 95 managed grassland plots (50×50 m) in real-managed landscapes. After controlling for site conditions in the analysis, we tested for significant differences between protected and non-protected grasslands and used a multi-group

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structural equation modelling (SEM) framework to investigate the linkages between land-use intensity, biomass and plant diversity.
Results In protected grasslands, plant diversity was significantly higher while forage production was significantly lower. In non-protected grasslands we found significantly higher land-use intensity, particularly in relation to mowing and fertilisation. Grazing intensity did not significantly differ between protected and non-protected grasslands. In non-protected grasslands we found a significant negative association between forage production and plant diversity. However, this effect was not significant in protected grasslands. We also found a negative association between land-use and plant diversity in both grassland types that was related to mowing and fertilising intensity. These two management aspects also influenced the positive association between land-use intensity and forage production. Furthermore, environmental conditions had a positive effect on forage production and a negative effect on plant diversity in protected grasslands.
Conclusions Our results confirm that the protection of grassland sites is successful in achieving higher plant diversity compared to non-protected grasslands and that protected grasslands do not necessarily trade-off with forage production. This is possible under moderate grazing intensities as higher land-use intensity has a negative effect on plant diversity, particularly on rare species. However, forage production is lower in protected sites as it is driven by mowing and fertilisation intensity. Future research needs to further investigate if the nature of these relationships depends on the livestock type or other management practices.

Keywords Natura 2000 · Plant species richness · Material nature's contributions to people · Provisioning ecosystem services · Land use intensity · Biodiversity conservation

Introduction

Human well-being critically relies on the Earth's resources and the protection and restoration of life-supporting systems (United Nations Environment Programme 2021). One of the most pressing global challenges is to meet the growing demand for food and feed while maintaining biodiversity's supporting functions that are required to ensure high and stable yields in the long-term (Seppelt et al. 2020; Savage et al. 2021). Grasslands provide numerous material, regulating, and non-material nature's contributions to people (NCP) and ecosystem services, such as forage for livestock, pest control, or aesthetic values (Petermann & Buzhdygan 2021). The reported benefits are often linked to plant species richness (Sanderson et al. 2004). Developing balanced human-nature interactions (Buonocore et al. 2018) that support plant diversity and ensure forage production (Rieb et al. 2017; Wang & Wang 2019) remains a challenge in European grasslands. Temperate grasslands are usually preserved through moderate disturbances in the form of grazing, mowing, or wildfires that disfavour woody plants (Pärtel et al. 2005; Habel et al. 2013; Keune et al. 2022). Thereby, low-intensity land-use has been favouring increasing biodiversity for millennia (Habel et al. 2013; Vellak et al. 2009). With increasing populations and growing demand for food, land managers have been pushed to manage their grasslands more intensively since the 1950s, (Seppelt et al. 2020; Mayel et al. 2021), turning grasslands into the fastest declining habitats in terms of extent and biodiversity in Europe and Eastern Asia (IPBES 2018). Simultaneously, a large proportion of pastures have been converted into cropland, causing overgrazing in remaining grasslands (Carlier et al. 2009). The production of livestock feed in the European Union (EU) has increased by more than 50% in the past three decades (IPBES 2018). The use of anthropogenic inputs, such as fertilisers, that affect both biodiversity and regulating NCP has risen (Foley et al. 2011; Bennett et al. 2021). In 2020, the EU's nitrogen fertiliser consumption was 6.9% and phosphorus consumption 21.9% higher than in 2010 (Eurostat 2022). Thus, more intensive land-use has led to the homogenization of ecological communities as it supports generalist species and negatively impacts habitat specialists (Bullock et al. 2011; Hudewenz et al. 2012). For instance, in 58% of British grasslands, the use of selective herbicides, nutrient addition, and reseeding as measures to increase livestock production have resulted in floristically species-poor grasslands and have had negative impacts on regulating NCP such as pollination (Bullock et al. 2011). Differing priorities regarding plant species diversity, forage quality and production lead to conflicts between farmers and nature conservationists (Pavlů et al. 2006) and have therefore been the object of NCP and ecosystem services research and practice.

Protected areas that exclude any human intervention have traditionally been used to preserve biodiversity and halt environmental degradation (Pärtel et al. 2005). Indeed, previous research has shown that high levels of biodiversity can be typically found in habitat types with a favourable conservation status (Silva et al. 2019). In temperate grasslands, however, it has been shown that minor management interventions can support species-rich habitats (Fülöp et al. 2021; Ostermann 1998; Silva et al. 2019). Pavlů et al. (2006) showed that plant species diversity increased within intensively and extensively grazed plots in comparison to unmanaged grassland plots in an experimental setting. Similarly, Hudewenz et al. (2012) found that greater resource availability may enhance plant diversity at low land-use intensity in contrast to high land-use intensity. Most evidence on the relationship between plant species richness and ecosystem functioning come from experimental sites (Petermann & Buzhdygan 2021), but this is yet to be proven in non-experimental sites, i.e., in real landscapes. Thus, the task is to find management solutions that offer synergistic effects in managed grassland ecosystems (Wang & Wang 2019) and thereby support both agricultural and nature conservation targets (Pavlů et al. 2006).

In this paper, we focus on the relationships between land-use variables and plant diversity and those between forage production and plant diversity. First, land-use intensity can support or harm biodiversity through different mechanisms. Moderate mowing and grazing may lead to higher plant species richness (Melts et al. 2018; Davidson et al. 2020). For instance, Fischer et al. (2009) suggest that, in order to support biodiversity, grazing intensity patterns may be reduced through, for example, low-intensity short rotations of livestock. Moderate mowing intensity may support plant species diversity by enhancing the flower cover or elongating the flower season through re-flowering (Hudewenz et al. 2012). Higher land-use intensity, in contrast, threatens plant species survival (Mayel et al. 2021; Savage et al. 2021). In particular, higher fertilisation rates, more frequent cutting and greater stocking rates reduce the number of plant species and lead to uniform plant communities (Sanderson et al. 2007). More frequent mowing can disturb resource availability and reduce structural complexity (Hudewenz et al. 2012). It is therefore plausible that grasslands in protected areas with lower land-use intensity show higher plant diversity than grasslands in non-protected areas. Second, high species-richness has been found to be linked to the efficient use of nutrients that can lead to stable biomass production (Melts et al. 2018). Discussions on the linkages between species richness and productivity such as the hump-shaped or unimodal productivity–biodiversity relationships (Guo and Berry 1998; Adler et al. 2011; Brun et al. 2019) remain controversial (Fraser et al. 2015; Mittelbach et al. 2001; Pierce 2014).

In this study, we provide further insights into the linkages between biodiversity and productivity by adding an important factor in real landscapes, namely the effect of the institutional framework of environmental protection guidelines in which these grasslands are placed. Thereby, our paper aims to provide new insights in the relationship between biodiversity and forage production by (i) analysing real-managed grasslands and (ii) considering the conservation context which is framed by legal institutions, such as the Birds Directive (2009/147/EC) and Habitat Directive (92/42/EEC) in Europe.

Therefore, we investigate (1) to what extent plant species diversity supports forage production in a range of managed grassland ecosystems, and (2) how this relationship varies between grasslands in protected and non-protected areas. We focus our work on three case study regions in Germany, where grasslands represent the second largest share of habitats in protected areas after forests (https://biodiversity.europa.eu), and host 40% of the endangered ferns and flowering plants (https://www.umweltbundesamt.de). These protected areas fall under national conservation laws or are part of the European Union's Natura 2000 network,[1] in which various agricultural-environmental programs established by nature conservation or agricultural administrations have aimed for the preservation and restoration of species-rich grasslands for several decades (Buchwald 2008).

[1] The Natura 2000 network includes areas protected under the EU's Habitats Directive (92/42/EEC) and the Birds Directive (2009/147/EC) (European Commission 2022).

Fig. 1 Map of the three case-study regions of the biodiversity exploratories in Germany (Memmert et al. 2022)

Materials and methods

Study site and data collection

We used data from 95 grassland plots (50×50 m) located in three regions of Germany that are part of the long-term research platform Biodiversity Exploratories (www.biodiversity-exploratories.de; Fischer et al. 2010). The grassland plots in the south-west region partly belong to the UNESCO[2] Biosphere Reserve Schwäbische Alb; those in the central region are located adjacent to the National Park Hainich (referred to as Hainich-Dün) and the grassland plots in the north-east region belong to the UNESCO Biosphere Reserve Schorfheide-Chorin (Fig. 1). Altitude (above sea level) ranges between 3 and 140 m in Schorfheide-Chorin, 285–550 m in Hainich-Dün, and 460–860 m in Swabian Alb. Annual mean temperature ranges between 8 and 8.5 °C in Schorfheide-Chorin, 6.5–8 °C in Hainich-Dün, and 6–7 °C in Schwäbische Alb. Annual mean precipitation ranges between 500 and 600 mm in Schorfheide-Chorin, 500–800 mm in Hainich-Dün, and 700–1000 mm in Schwäbische Alb (Fischer et al. 2010). Data on land-use intensity, plant species richness, biomass and site conditions were retrieved from the Biodiversity Exploratories Information System (BExIS) (https://www.bexis.uni-jena.de) (see SI1 for a data overview). The selection of variables was based on their relevance for our hypothesised relationships, their use in previous studies on grassland ecosystems in our study site (e.g. Allan et al. 2015; Le Provost et al. 2021) and the availability of data.

Data on protection status was retrieved through spatial analysis in GIS. The majority of plots in protected areas only belong to a Natura 2000 site (69%), while 29% of plots in protected areas belong to both nationally protected areas (German: *Naturschutzgebiet*) and Natura 2000 sites. As we did not find significant differences between land-use variables, plant diversity, forage production and most site condition variables when separating plots into national protection areas and EU's Natura 2000 sites (SI3), we decided to merge the data sets and treat these plots as a single group representing protected areas. Therefore, our dataset comprised 43 grassland plots inside protected areas and 52 grassland plots outside protected areas.

All data was processed using R software version 4.2.2 (R Core Team 2022). We obtained data on plant cover for 368 different plant species for a range of available years (i.e. 2008–2018) (see SI11 for an overview of most abundant species). We calculated the Effective Number of Species based on the Shannon Index as a diversity measure (Jost 2006; Jost et al. 2010), as it is more sensitive to the presence of rare species (which is the purpose of grasslands protection in Natura 2000 sites). To allow for comparison, we additionally calculated the Effective Number of Species based on the Simpson Index. Calculations were done using the *diverse* package (Guevara et al. 2017).

For forage production, we used the mean value of dry biomass for all available years to avoid potential seasonal bias (2009–2018). Biomass was sampled by cutting the biomass at the height of 4 cm before the first mowing or before grazing, then it was dried in

[2] United Nations Educational Scientific and Cultural Organisation.

the oven at 80 degrees for 24 h and weighed. To avoid strong disturbances the biomass was cut at a different position each year (see Hinderling et al. 2023).

In order to compare across the different management regimes applied in our plots, we used an index composed of grazing, mowing and fertilisation data combined to obtain a single land use intensity metric. Grazing intensity refers to livestock units (i.e. cattle, horses, sheep, goats) per hectare and days of grazing. Mowing intensity refers to the number of cuts per year. Fertilisation intensity is based on the amount of applied nitrogen within the fertiliser per hectare (see Blüthgen et al. 2012; Manning et al. 2021; Ostrowski et al. 2020). Land-use intensity data was collected through annual land-use surveys (Vogt et al. 2019). Here, we used land-use intensity data from 2006 to 2017 to capture land-use management over time and match biomass records (Le Provost et al. 2021, Manning et al. 2021). Data on grassland suitability including soil pH, soil depth, soil sand and clay content, slope, elevation and the Topographic Wetness Index (TWI) was retrieved for the latest available year (SI1). All data was normalised and scaled using the *bestNormalize* (Peterson 2022) and *scales* (Wickham & Seidel 2022) packages in R (R Core Team 2022).

Analysis

All analyses were run using R software version 4.2.2 (R Core Team 2022). For our main analysis, we excluded plots from the UNESCO Biosphere Reserve Schorfheide-Chorin as they all belonged to a Natura 2000 site, and hence, did not provide counterfactuals for the non-protected status. This led to a dataset containing 80 plots. We tested for significant differences between plots in protected and non-protected grasslands through Student's *t*-Test and used the violin plots from the R package *ggplot* (Wickham 2016) for visualisation. We also analysed *spearman's correlations* between all variables (including the three components of the land use intensity index) using the R package *corrplot* (Wei & Simko 2021; SI4).

Next, we constructed the latent variable *condition* defined by our indicators soil depth, Topographic Wetness Index, sand content, elevation, and slope. The environmental variables soil pH and soil clay were excluded from the latent variables as this improved the model fit. Then, we fitted a multi-group structural equation model (SEM) for the two groups (i.e. protected and non-protected sites) using the R package *lavaan* (Rosseel 2012).

As our data did not fit a multivariate normal distribution, we used the *maximum likelihood estimation* as a robust procedure (Yuan et al. 2000; Andreassen et al. 2006). We compared different model fits by releasing parameter constraints in sequence and comparing modification indices based on the difference of a constrained versus a free model. For each constraint it was considered whether releasing the parameter would align with theoretical knowledge. We tested and established configural, metric, scalar and strict invariance (Bialosiewicz et al. 2013; van de Schoot et al. 2012) by comparing the goodness-of-fit indicators for chi-square, Comparative Fit Index (CFI), Tucker Lewis Index (TLI) and Root Mean Square Error of Approximation (RMSEA) (Hu and Bentler 1999; Schumacker and Lomax 2010, SI2). Using the proposed cut-off criteria for CFI, TLI and RMSEA tends to over-reject true-population models at small sample size (<200). Therefore, we additionally used the chi-square divided by the degrees of freedom (χ^2/df) as a measure of model fits (Anderson and Gerbing 1984) for all our SEMs.

In addition, we ran a separate analysis using the Effective Number of Species based on the Simpson Index (SI6). As results were largely the same (except the negative links between land-use intensity and plant diversity, plant diversity and forage in non-protected plots that turned not significant), we show only the results based on the Shannon index in the main text.

To investigate potential regional differences in protected grasslands, we ran a separate SEM including only the plots belonging to protected areas from all three regions, including the UNESCO biosphere reserve Schorfheide-Chorin (SI7) using a total of 43 plots.

In addition, to test for potential differences in the effects of the individual components of the land use intensity index, we ran the SEM analyses separately for each of the three indicators (mowing, fertilisation and grazing) (SI 8–10).

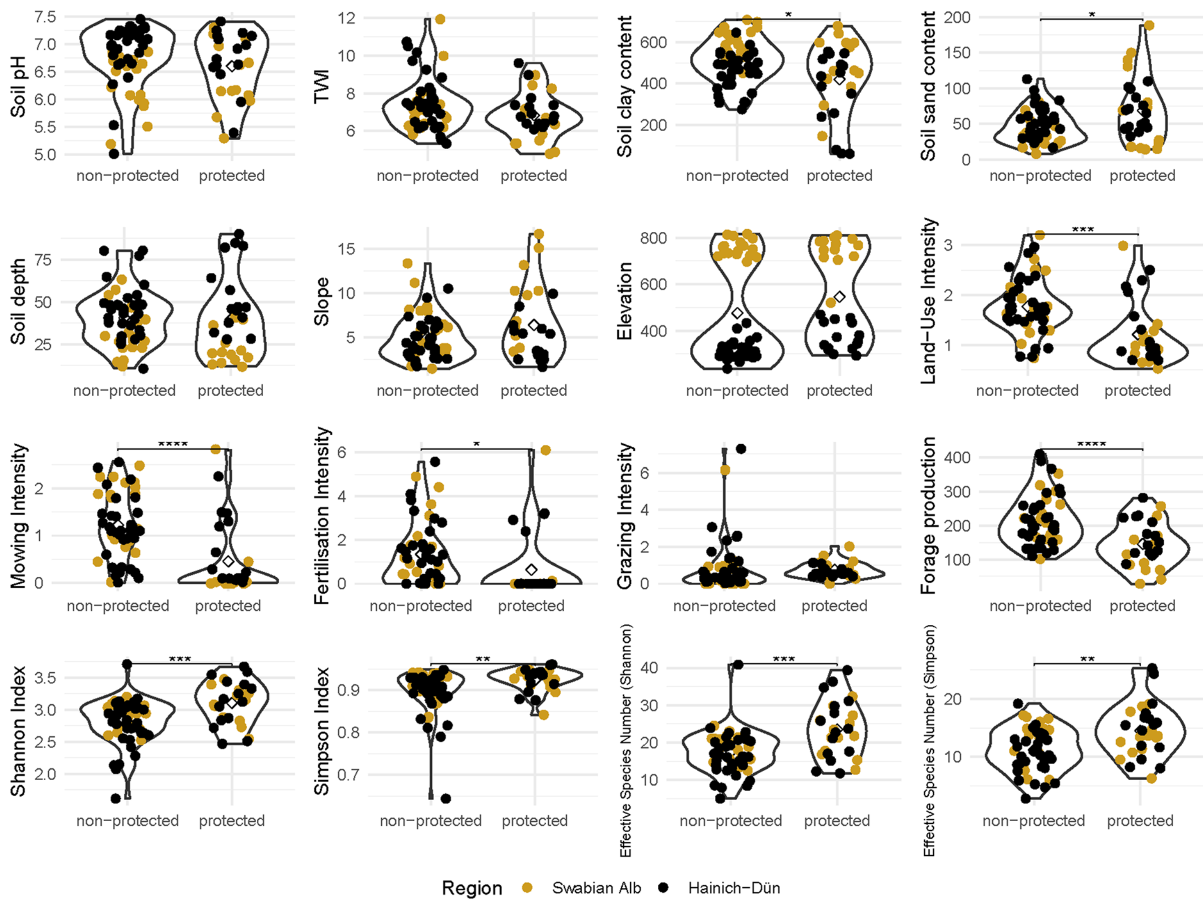

Fig. 2 Comparison of sites within and outside protected areas with regards to site condition and land-use intensity. Black dots indicate data points from Hainich-Dün (48 plots) and gold dots from Schwäbische Alb (32 plots). Shapes indicate the density of data points for each protection status. (Student *T*-test results, significance levels: * for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$)

Results

Differences between protected and non-protected grasslands

Mowing intensity, fertilisation intensity, and overall land-use intensity were significantly higher in plots in non-protected grasslands in comparison to plots located in protected grasslands (Fig. 2). Grazing intensity did not significantly differ between protected and non-protected sites. Regarding other key variables, plant diversity was significantly higher in plots of protected grasslands while forage production was significantly higher in plots belonging to non-protected grasslands. Differences in site condition variables were only significant for soil clay and sand content, which had a larger range of values in protected grasslands (Fig. 2).

Modelled links between land-use intensity, plant diversity, forage and site condition variables

We found that, in both protected and non-protected grasslands, land-use intensity was positively associated with forage production but negatively associated with plant diversity (Fig. 3). In non-protected grasslands, plant diversity and forage production were negatively linked while this association was not significant in protected sites. In addition, for protected grasslands our results depict a positive link between *condition* and forage production. Our sensitivity analysis using individual land-use variables revealed that

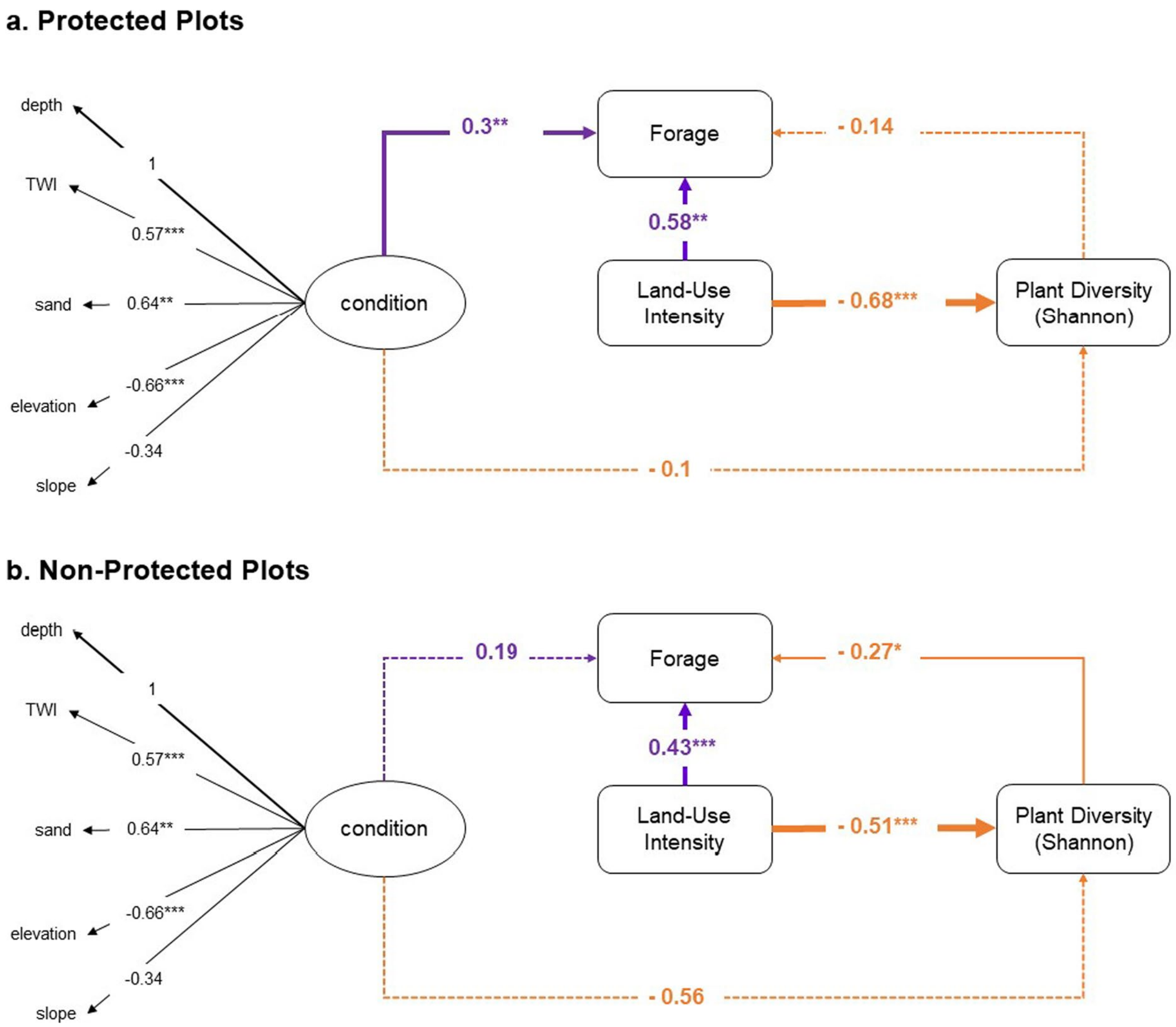

Fig. 3 Multigroup SEM showing the linkages between the site condition of the plot, land-use intensity index, forage production, and plant diversity in **a** protected and **b** non-protected plots. Orange lines present negative regression coefficients while purple lines present positive coefficients. Solid lines indicate significant linkages and dashed lines non-significant effects (Significance levels: * for $p \leq 0.05$, ** for $p \leq 0.01$, *** for $p \leq 0.001$). Note that boxes on the left-hand side show the six indicators of the latent variable *condition* and that all latent-variable indicators are significant (except for *soil depth* which is a fixed parameter)

the positive association between land-use intensity and forage production could be mainly explained by mowing and fertilising intensity (SI8; SI9). When fitting a separate model with grazing intensity only, the linkage of grazing intensity and forage production is much lower in magnitude and non-significant (SI10). Furthermore, the sensitivity analysis showed that the negative association between land-use variables and plant diversity is only significant and negative for the model fits using mowing and fertilising. When fitting the data using grazing intensity the linkage with plant diversity becomes non-significant. For protected grasslands, this linkage is positive yet non-significant.

When running a separate SEM with plots belonging only to protected grasslands for all three regions, the link between land-use intensity and forage production remained positive (0.54***) (SI7) while the link between land-use intensity and plant diversity remained negative (− 0.52***). The negative link between plant diversity and forage production stays negative yet non-significant (− 0.07). The latent variable *condition* shows strong significant linkages with forage production and plant diversity.

Discussion

In this study we show that land-use intensity drives the relationship between forage production and plant diversity in grasslands and that this is mediated by mowing and fertilisation intensity. Importantly, the trade-off between forage production and plant diversity found in non-protected sites seems to be alleviated in protected grasslands, as it becomes non-significant. This trade-off was also non-significant when considering a diversity index less sensitive to rare species (SI6).

Our results show that grassland plots in protected areas are successful in protecting biodiversity in terms of plant species diversity while allowing similar grazing intensities as non-protected grasslands. Apart from management effects, the site conditions play an important role in these observations and vary between protected and non-protected grasslands. For example, protected grasslands seem to have adequate soil conditions for biomass production, although non-protected grasslands are still more productive.

Management effects on grassland plant diversity

In line with our expectations, our results showed that plant diversity was significantly higher in protected grasslands (Fig. 3) as, in general, habitat types with favourable conservation status host high levels of biodiversity (Silva et al. 2019). In addition, the negative association between land-use intensity and plant diversity appeared to be driven by fertilisation and mowing intensity, even in protected grasslands where these variables were significantly lower. These results partially align with those by Allan et al. (2014), who in the same sites showed that declines in the average proportional species richness across taxonomic groups could be best explained by mowing (and grazing intensity) rather than by fertilisation intensity. However, as mowing and fertilisation intensity are strongly correlated in our case-study sites, deriving conclusions on the individual effects of the land-use variable needs to be done with caution. Other studies suggest that, in line with our results, meadows with low mowing intensities and without any fertilisation seem to have higher biodiversity values (Mayel et al. 2021). Moderate mowing intensity may support plant species diversity by enhancing the flower cover or elongating the flowering season through re-flowering while higher mowing intensity disturbs structural complexity (Hudewenz et al. 2012). Regarding fertilisation intensity, nutrient inputs in fertilised plots, such as cumulative N input, can increase the biomass of generalist species and decrease the biomass of rare or threatened species (for an overview see Melts et al. 2018).

Another option to support biodiversity is to reduce grazing intensity patterns through, for example, low-intensity short rotations of livestock (Fischer et al. 2009). Indeed, although grazing is promoted by the Natura 2000 guidelines, we did not find significantly higher values for grazing intensity in protected grasslands in our main analysis. Moreover, in our sensitivity analysis, grazing intensity showed a positive yet non-significant linkage with plant diversity (SI10) for protected plots. At higher intensity, grazing can be a driver for biodiversity loss. The trend of increasing loss of vegetation cover in intensive grazing regimes can cause evaporation and thereby upward movement of water and soluble salts in the soil. Accumulated salt in the top horizon can lead to a decrease in vegetation growth (Mayel et al. 2021). Furthermore, the more aboveground plant biomass is consumed by livestock, the less plant litter is present on the surface and fewer residues can be incorporated into the soil. This affects the soil water and temperature content, which in turn affects soil organic C and soil biological activity. At light grazing intensities, the soil may recover through the growth and decomposition of plants and roots or the activities of soil microorganisms (Mayel et al. 2021). Our sensitivity analysis for protected grassland plots revealed that the negative linkage between overall land-use intensity and plant diversity was reduced in magnitude in comparison to our main analysis with plots from both protected and non-protected sites. This finding could suggest that appropriate grazing activities could be more beneficial for biodiversity than other land-use management strategies. In contrast, significantly higher mowing and fertilisation in non-protected grasslands may be responsible for observed biodiversity losses in comparison to protected sites.

The positive effect of grazing on biodiversity has been shown for different grassland environments. For instance, in the tallgrass prairie of North America, moderately grazed plant communities are more species rich than ungrazed or intensively grazed communities due to structural heterogeneity and limited defoliation by livestock (Fuhlendorf and Engle 2001). An experimental study in the Great Plains (USA) showed that, at the plot level (10 m^2), under bison grazing native species richness was 103% higher and under cattle grazing 41% higher when compared to ungrazed plots (Ratajczak et al. 2022). Furthermore, using a standardised survey at 98 sites across six continents, Maestre et al. (2022) found that in drylands, increasing grazing pressure shifts the relationships between plant species richness and aboveground biomass from negative to positive at the plot level (45 × 45 m). The effects of grazing on biodiversity, however, remain context-dependent as the results of the interactions between grazing pressure and abiotic and biotic features cause some uncertainty on the effects of grazing on ecosystem services and nature's contributions to people (Maestre et al. 2022).

Furthermore, at the plot level, we found a positive association between mowing and fertilising intensity and biomass production, while grazing was positively associated with plant diversity in protected areas. Zooming out to a landscape perspective, this implies that a 'land sparing' strategy (high-intensity grasslands on a small land footprint) may reconcile productivity and biodiversity at the landscape level. Hence, non-protected grasslands deliver forage through mowing and fertilising and non-protected grasslands maintain biodiversity through grazing. Hypotheses on the biodiversity-productivity relationship at the landscape level, however, require further testing as multiple mechanisms aside the land-sparing versus land-sparing dichotomy come into play at this spatial scale. For instance, whether negative land-use impacts on the plot scale could be buffered by landscape level mechanisms such as recolonization of species from diverse surrounding habitats needs to be further explored (Öster et al. 2007). For instance, Le Provost et al. (2021) found that vascular plant diversity was negatively impacted by the permanency of surrounding grasslands and forests and positively, yet insignificantly, affected by the forest cover and land cover diversity at the landscape level in our study sites. Further research could investigate how these landscape mechanisms play a role in protected versus non-protected areas. For instance, negative spill-over effects of the application of fertilisers and herbicides on agricultural fields adjacent to conservation areas (Köthe et al. 2023) and positive spill-over effects from natural areas to managed grasslands (Blitzer et al. 2012) could be tested in non-experimental managed grasslands.

The significant negative linkage between land-use intensity and plant diversity, in both non-protected and protected plots, highlights the need to moderate land-use intensity to reduce the negative influence of human activities on biodiversity in grasslands and minimise trade-offs. Based on a simulation approach, Neyret et al. (2021) found that trade-offs between ecosystem services such as fodder production and carbon storage persist in high- and low-intensity grasslands while multifunctionality in terms of ecosystem services diversity can be achieved when a moderate level of ecosystem services supply is accepted by stakeholders.

Insights for the diversity-productivity debate

Our SEM analysis showed that the trade-off between biomass and plant diversity was only significant in non-protected grasslands and especially relevant for rare species, as using a Simpson-based diversity index instead of a Shannon-based one did not yield significant effects (SI6). Similarly, we found a negative correlation between forage production and plant diversity (SI4). This contrasts with studies suggesting that improving grassland species richness can increase forage production. In temperate grasslands, for instance, the occupation of different niches by distinct species often results in improved resource utilisation over space and time (Sanderson et al. 2004). Additionally, interactions between legumes and other plants have been found to affect nitrogen availability which in turn improves productivity (Sanderson et al. 2004; Savage et al. 2021). Previous research in our case-study sites found that changes to the plant community including diversity declines were key mediating factors by which land-use intensity indirectly affected ecosystem multifunctionality (Allan et al. 2015). Likewise, Isbell et al. (2011) found that 84% of 147 grassland plant species analysed in 17 biodiversity experiments supported ecosystem functions at least once and were therefore relevant for sustaining ecosystem services. Hence, evidence from other studies does not necessarily confirm the negative linkages between biodiversity and productivity that we found here. In general, there are different hypotheses on the shape of the productivity-plant species richness relationship (Adler et al. 2011) and the mechanisms behind these shapes are still under investigation (Grace et al. 2016). Still, our study provides evidence that these relationships are most likely associated with the management practices in real-world grasslands.

In addition, our sensitivity analysis with only protected sites revealed that the magnitude of the effect of land-use intensity on forage production is substantially higher than in the multi-group SEM results. These results indicate that the management of grasslands differs between protected areas across Germany, and that these differences in management may affect the diversity-productivity relationship in real managed grasslands. For instance, a higher grazing intensity in the UNESCO Biosphere Reserve Schorfheide-Chorin paired with rich organic soil may balance the linkages towards a positive diversity-productivity relationship. This supports the findings of other studies in our case-study region highlighting the careful consideration of regional environmental differences when attempting to generalise land-use effects on species diversity (Socher et al. 2012).

Our study also points to the limitation of studying the relationship of biodiversity and productivity in real landscapes. For instance, as non-productive sites may be of lower economic value they may be set aside for biodiversity conservation. Arguing from another perspective, highly biodiverse grasslands may be put under environmental protection to conserve already existing plant diversity. However, this may not be true for all protected ecosystems, as former intensively used grasslands can also be targeted for ecological restoration or set aside for conservation through environmental commitments at the policy level.

In this paper we assumed that relationships between biodiversity and forage provision can be measured on a plot scale-i.e. 50×50 m. These relationships may also be detectable and synergies between biodiversity and productivity desired at larger landscape scales where factors such as landscape heterogeneity are relevant drivers of biodiversity. Theory suggests that heterogeneous landscapes with a diversity of suitable habitats contain a species pool with higher species richness due to seed dispersal and pollen flow (Gaujour et al. 2012). For instance, it was shown for the Great Plains in the United States that restoring heterogeneity within a landscape through grazing-fire interactions can increase plant diversity (Fuhlendorf and Engle 2001). Studies on the effects of landscape heterogeneity on plant diversity, however, show mixed results and some plant species may be unaffected by landscape heterogeneity (Gaujour et al. 2012). Nonetheless, many scholars advocate for management paradigms that consider landscape heterogeneity within rangelands and permanent grasslands (Fuhlendorf and Engle 2001; Tscharntke et al. 2012; Harlio et al. 2019).

From a policy perspective, maintaining higher biodiversity at a landscape level cannot be achieved by a single farmer or conservation measure at the farm level (Gaujour et al. 2012). Conservation schemes, thus, need to acknowledge the joint effort of several farmers required to manage the landscape in its entirety (Landis 2017; Westerink et al 2017).

Limitations & outlook

In this study, we evaluated the effectiveness of managed grasslands in maintaining plant diversity and yielding high productivity. However, there are other criteria for evaluating the potential benefits of biodiverse grasslands. These include the seasonal distribution of yields, the comparison of input costs to achieve productivity, and the provision of other NCP and ecosystem services including improved wildlife habitat and landscape aesthetics (Sanderson et al. 2004; Schmitt et al. 2022).

We are aware that we used a simplified representation of managed grassland ecosystems in this study and that other constituents of grasslands, such as belowground biodiversity and functions may influence plant diversity and forage production. As grasslands are associated with high plant species richness, we focused on plant diversity as an indicator of biodiversity. Other biodiversity indicators such as pollinators or bird species (Petermann & Buzhdygan 2021) could be considered in future analyses. Besides, we only investigated plant diversity as a driver of productivity. Future studies could investigate which species might be especially relevant as a mediating factor of land-use intensity linkages and forage production. However, in line with the precautionary principle, all species should be conserved as uncertainty regarding the role of specific species in the provision of NCP remains (Isbell et al. 2011).

Our latent variable site conditions might only capture a selection of relevant indicators, as the range of soil conditions analysed appeared to be larger in protected grasslands, which could potentially drive some of these results. While conclusions on the magnitude and direction of the described relationships have to be drawn with caution, it is important to highlight that the linkages of plant diversity and productivity depend on the underlying environmental conditions in which protected and non-protected grasslands are placed and assessed.

This study relied on available land-use data which could limit a deeper understanding of land management effects in our case-study sites. For instance, we used total livestock units per hectare as a measure of grazing intensity without distinguishing among grazer types. Previous studies have shown that intensive grazing regimes with only one herbivore species can negatively impact biodiversity, while multiple different grazing animals with different foraging strategies may contribute to more biodiverse grasslands (Fraser et al. 2014, 2022; Freschi et al. 2015). Moreover, we did not consider other management characteristics that may affect grasslands' biodiversity, such as re-seeding (Sanderson et al. 2004; Hyvönen et al. 2021) or the type of mowing head used (Steidle et al. 2022). Despite this limitation, zooming into the linkages of land-use intensity in real-managed grasslands delivered useful insights into the relevance of environmental protection status for plant diversity and forage production.

Our results show differences in land-use intensity, forage production and biodiversity across the protected sites. This highlights the importance of combining biophysical analyses with environmental policy analyses. The impacts of agricultural and environmental regulations need to be disentangled from individual land managers' motivations and practices (see e.g. Hauck et al. 2014; Bouwma et al. 2018; Metzger et al. 2021). Furthermore, having identified significant linkages within the ecosystem, the next step would be to explore how managers' motivations and values, including the co-production of NCP (Kachler et al. 2023), explain land management strategies and their effects observed in our model. We therefore suggest combining biophysical data on the plot or field level with survey data about land users and their management strategies. This would not only facilitate a better understanding of how NCP and ecosystem services are provided in managed grasslands but also help to identify leverage points for policymakers to promote multifunctional land management at the landscape level. In general, as landscape strategies are highly sensitive to the prioritisation and demand for NCP by stakeholders, it is crucial to apply participatory approaches in the development of land management strategies (Neyret et al. 2021).

Conclusion

Our study provides new insights in the relationship between biodiversity and forage production by (i) analysing real-managed grasslands and (ii) considering the conservation context which is framed by legal institutions such as the Birds Directive and Habitat Directive in Europe.

This study provides evidence of the role of land-use intensity in driving the relationship between forage production and plant diversity in grasslands. In particular, we showed that the trade-off between forage production and plant diversity found in non-protected sites was not further significant in protected grasslands or when considering a diversity index less sensitive to rare species.

Our results support that moderate levels of grazing in protected grasslands can balance forage production with biodiversity conservation, while high levels of mowing and fertilisation decrease plant diversity. While hypotheses need to be tested at the landscape level, our study supports recommendations at the plot level to moderate anthropogenic inputs as a means to reduce trade-offs and maintain a healthy biodiversity-productivity balance.

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Data availability This work is based on data elaborated by several projects of the Biodiversity Exploratories program (DFG Priority Program 1374). The datasets are publicly available in the Biodiversity Exploratories Information System (http://doi.org/10.17616/R32P9Q), (ID 31018, ID 20826, ID 27087, ID 26106).

Declarations

Competing interests The authors declare no competing interests.

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