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Grassland management in Germany: effects on plant diversity and vegetation composition

Grünlandnutzung in Deutschland: Auswirkungen auf Pflanzendiversität und Vegetationszusammensetzung

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Abstract

The vast majority of European grasslands strongly depend on the regular removal of aboveground biomass by agricultural land use, mostly grazing or mowing or a combination of both. These specific management schemes have strong influence on plant diversity and vegetation composition, depending on their particular characteristics and their intensity. For example, the presence or absence of fertilization will favour some species over others, changing plant communities accordingly. Additionally, the farmer's choice of a specific management scheme will also depend on the abiotic site conditions. This leads to a complex set of associated factors potentially affecting the structure and diversity of grasslands.

In this study, we compiled a unique dataset of 169 differently managed grasslands (in total 202 plots), which were sampled in five regions across Germany. For each plot, we documented management characteristics, measured plant diversity and functional group composition, recorded endangered species according to red lists, and calculated Ellenberg indicator values. We assessed patterns in vegetation composition and diversity in relation to the particular management scheme, which was categorized as meadow, meadow with autumn or winter grazing (with mowing as predominant management), mown pasture (where mowing and grazing are used at roughly equal intensity), seasonal pasture (with grazing as predominant management) and year-round pasture.

Our study showed that grasslands of different management schemes significantly differed in diversity, structure and functional composition. However, it also became obvious that vegetation composition was not strictly distinguished by management alone. Local and regional characteristics such as soil conditions, size of the grassland species pool or land-use history, often played a more prominent role than land use alone. Assumingly, the interplay of those local and regional characteristics with the proportion of grazing and mowing at a particular site inhibit clear differences among our predefined management schemes. Nevertheless, species richness was the lowest in year-round pastures, moderate in meadows and highest in seasonal pastures. In contrast, year-round pastures harboured the highest mean numbers of endangered species. The dependency of a certain management scheme on site-specific environmental factors such as soil fertility, further complicated the clear separation of management effects from those of the environmental background.

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In summary, modern grassland management strongly shaped grassland vegetation, but today's combination of different management practices complicated the assessment of specific land-use effects on plant diversity. Thus, neither mowing nor grazing turned out to be "the one and only" management for nature conservation. Although our results challenge long-term prognoses for future vegetation development under modern grassland management, we clearly showed that low-intensity management and the absence of fertilization promoted plant diversity, with higher values in pastures compared to meadows and mown pastures.

Keywords: endangered plant species, fertilization, grassland conservation, grazing, mowing, productivity

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

The vast majority of European temperate grasslands is of anthropogenic origin and thus strongly depends on the regular removal of aboveground biomass (FISCHER & WIPF 2002). For centuries, grasslands were primarily grazed and only to a lower extent degree used for haymaking (POSCHLOD et al. 2009). In the absence of anthropogenic fertilization, most sites impoverished in nutrients and grasslands extremely rich in plant and animal species developed (VEEN et al. 2009, WILSON et al. 2012). However, since the 1950/60s, many grasslands have been either abandoned or their management has been strongly intensified, resulting in severe changes in vegetation composition and structure and in the loss of grassland biodiversity in many places (WESCHE et al. 2012). This land-use change is still ongoing in most European regions (KÜMMERLE et al. 2016). While the intensification of management especially applied to grasslands on nutrient-rich soils, those on low productive or less well accessible sites were often abandoned or afforested (CRITCHLEY et al. 2003, COUSINS & ERIKSSON 2008). Due to their richness in species and important ecosystem services (ALLAN et al. 2015), grasslands are particularly valuable habitats that are in the focus of nature conservation and ecosystem restoration (VEEN et al. 2009). However, today's European grasslands strongly vary in vegetation composition, structure and diversity and thus in conservation value. Currently, there is an enormous variety in management schemes, aims, techniques and intensities, ranging from intense use with high fertilization levels of improved grasslands to low-intense traditional management of mainly less fertile and/or remote sites (BLÜTHGEN et al. 2012). Whereas the latter are mostly used as pastures, grasslands on more productive sites are more intensively managed by mowing or grazing or a combination of both (SOCHER et al. 2012). The specific management scheme has various impacts on plant diversity and vegetation composition but also on faunal taxa (e.g., ZECHMEISTER et al. 2003, KLAUS et al. 2013a, ALLAN et al. 2014, BOCH et al. 2016, KRUSE et al. 2016). Whereas mowing leads to a uniform removal of plant biomass at a certain time, grazing is selective at different levels (landscapes, habitats/vegetation types, single plants, parts of plants) (ROOK & TALLOWIN 2003). In contrast to mowing, grazing leads to the creation of gaps through trampling and wallowing of livestock within otherwise densely closed swards (ROSENTHAL et al. 2012, LORENZ et al. 2016). As a consequence, grazing promotes the establishment and maintenance of low growing and light demanding species (FLEISCHER et al. 2013, KÖHLER et al. 2016, RUPPRECHT et al. 2016). However, it is still strongly debated whether mowing or grazing is the better tool to maintain grassland plant diversity (e.g., TÄLLE et al. 2015, 2016, KRUSE et al.

2016). Besides management intensity other factors such as abiotic site conditions, site history and species pools and the interplay of these factors with management strongly influence vegetation composition and structure in a hardly predictable way.

As land-use change and intensification are assumed to be the major drivers of the current biodiversity loss (SALA et al. 2000, NEWBOLD et al. 2015), it is important to understand patterns in vegetation composition and diversity in relation to grassland management and its specific schemes. However, especially large-scale studies including differently used grasslands with their major environmental characteristics are scarce. Therefore, we studied 202 grassland plots under different management schemes - categorized as meadow, meadow with autumn or winter grazing, mown pasture, seasonal pasture and year-round pasture - to assess land-use and site effects on vegetation composition and plant diversity. In detail, we asked the following questions: (1) Do vegetation composition, plant functional groups, plant diversity and endangered species occurrence differ among management schemes? (2) Is mowing or grazing more beneficial for the conservation of plant diversity in grasslands? (3) Which further (environmental) factors influence plant diversity and endangered species numbers in the studied grasslands?

2. Study area

We sampled 202 plots within 169 differently managed grassland sites from five geographic regions in Germany, which in one case also included grasslands in the bordering Netherlands (Fig. 1, Table 1). In each region, we sampled 15 to 50 plots (Table 2). Three rather comprehensive study regions are part of the *Biodiversity Exploratories* project for

Fig. 1. Locations of the study regions in Germany. Dotted lines connect cohesive sub-areas of lager regions. See also Table 1.

Abb. 1. Untersuchungsgebiete in Deutschland. Gepunktete Linien verbinden einzelne Teilgebiete. Siehe auch Tabelle 1.

Table 1. Environmental conditions of the five study regions (from FISCHER et al. 2010, DWD 2013, RUPPRECHT et al. 2016).

Tabelle 1. Umweltbedingungen der fünf Untersuchungsgebiete (nach FISCHER et al. 2010, DWD 2013, RUPPRECHT et al. 2016).

	Region				
	Central	North	Northeast	Northwest	Southwest
Toponym	Hainich-Dün	Friesland-Hamburg	Schorfheide-Chorin	Niederrhein-Westfalen	Schwäbische Alb
Geology	Calcareous bedrock with loess layer	Young glacial landscape with sandy ridges and fens	Young glacial landscape with sandy ridges and fens	Merly and sandy areas on chalk plain	Calcareous bedrock with loam layer
Elevation	285–550 m	12–45 m	3–140 m	35–160 m	460–860 m
Annual mean temperature	6.5–8° C	8.2–9.6 °C	8–8.5 °C	9.2–10.5 °C	6–7 °C
Annual mean precipitation	500–800 mm	750–900 mm	500–600 mm	750–850 mm	700–1000 mm

functional biodiversity research (FISCHER et al. 2010; www.biodiversity-exploratories.de): the UNESCO Biosphere Reserve *Schorfheide-Chorin* in Northeast Germany, the National Park Hainich with surroundings in the center (called *Hainich-Dün*) and the UNESCO Biosphere Area *Schwäbische Alb* with surroundings in the southwest of Germany (Fig. 1). Moreover, two regions in northwestern Germany with more distant plots were studied: *Friesland-Hamburg* in the very north and *Niederrhein-Westfalen* in the northwest of Germany. While the most northern and western regions exhibit oceanic to sub-oceanic climate with rather cool summers and mild winters, there is a climatic gradient of decreasing precipitation and slightly lower annual mean temperatures towards the more continental northeastern region. There is also a gradient of rising altitude from north to the south. While the northern and western regions were lowlands or undulating landscapes not more than 140 m a.s.l, the central and the southwestern region were low mountain ranges on calcareous bedrock. All grasslands had a slope of less than 20% and none is permanently waterlogged. With the exception of the northwestern region, where also drained fen soils (histosols) occurred, grasslands were on mineral soils (Table 1).

Most of the studied agricultural grasslands belonged to *Arrhenatherion elatioris* W. Koch 1926 and *Cynosurion cristati* Tx. 1947 communities, with transitions to *Polygono-Trisetion* Br.-Bl. et Tx. ex Marschall 1947 nom. invers. propos., *Calthion* Tx. 1937 and *Magno-Caricion elatae* W. Koch 1926 communities, depending on altitude and soil moisture. Additionally, *Bromion erecti* Koch 1926 communities occurred on shallow calcareous soils. On year-round pastures several different vegetation types were found within one complex. Communities of the alliances *Cynosurion cristati*, *Arrhenatherion elatioris*, *Arction lappae* Tx. 1937, *Calthion* and *Magno-Caricion elatae* were frequent, while on nutrient-poor sandy soils *Ericion tetralicis* Schwickerath 1933, *Genisto-Callunion* Böcher 1943, *Corynephorion canescentis* Klika 1931, *Koelerion arenariae* Tx. 1937 and *Thero-Airon* Tx. ex Oberdorfer 1957 communities were also present.

Nomenclature of plant species follows WISSKIRCHEN & HAEUPLER (1998).

3. Material and methods

3.1 Field and laboratory work

In general, management varied strongly among grasslands in our study but is representative for large parts of Central European landscapes. We distinguished between five different management schemes (Table 2):

1) *year-round pastures*, where mostly mixed herds of cattle and horses graze a complex of open habitats at low stocking densities of not more than 0.6 livestock units per ha
2) *seasonal pastures* ungrazed during winter (grazing-only systems sometimes with an irregular mulching cut at the end of the season)
3) *mown pastures*, where hay making (1–3 cuts) and grazing are combined or annually alternated at roughly similar intensity levels
4) *meadows with autumn or winter pasture* at rather low grazing intensity so that mowing is the predominant management (1–3 cuts)
5) *meadows* which are solely mown (mostly two to three cuts, rarely just one cut per year).

We also assessed whether grassland management included organic and/or mineral fertilizer applications or not. Data was gathered for at least the respective sampling year of each site (2012 or 2013) or as a mean of consecutive years by interviewing farmers and land owners (BLÜTHGEN et al. 2012). In all grasslands, except year-round pastures and some grazed grasslands, we sampled one plot in the center of the site. Most of the year-round pastures and seasonally grazed grasslands in the northern and northwestern study regions are quite spacious and comprised different vegetation types within one site, ranging from dry sand grasslands to moist depressions and tall forb communities. To cover the complete structural diversity, we sampled one plot per vegetation type (three to four different types per year-round pasture, two different types in seasonal pastures). Finally, we collected data on 202 plots from the 169 different grassland sites/complexes (Table 2).

Vegetation was recorded from mid-May to the beginning of July 2013, except in the northwestern region where sampling took place already in 2012. We assessed the presence and percentage cover of all vascular plant species on 4 m × 4 m plots and harvested aboveground biomass as mixed samples of randomly placed replicates, either of four 0.25 m^2 or five 0.1 m^2 quadrats. Occasionally occurring taller shrubs, bryophytes and litter were excluded from biomass sampling. Except of year-round pastures, biomass was sampled prior to mowing and/or grazing management.

Table 2. Numbers of differently managed grasslands in the five study regions in Germany. Numbers in brackets give the numbers of study plots if different from the number of grassland sites (only true for year-round pastures and seasonal pastures where more than one plot was studied per site according to different vegetation types within the large pastures).

Tabelle 2. Anzahl unterschiedlich genutzter Grünländer der fünf Untersuchungsgebiete in Deutschland. Angaben in Klammern: Anzahl der Aufnahmeflächen, die im Fall von Ganzjahresweiden von der Anzahl der Grünlandflächen abweichen können (mehrere Aufnahmen pro Ganzjahresweide-Fläche).

	Study regions					
Management	Central	North	Northeast	Northwest	Southwest	Total
Year-round pastures	1	4 (14)	0	11 (31)	0	**16 (46)**
Seasonal pastures	18	1	20	4 (7)	14	**57 (60)**
Mown pasture	20	0	11	0	14	**45**
Meadow with autumn or winter pasture	8	0	4	0	3	**15**
Meadow	3	0	14	0	19	**36**
Total	50	5 (15)	49	15 (38)	50	**169 (202)**

3.2 Data analyses

We calculated mean cover weighted Ellenberg indicator values for nutrients (Ellenberg N), moisture (Ellenberg M) and soil reaction (Ellenberg R) for each plot (ordinal scale ranging from 1 to 9; see ELLENBERG et al. 2001). The number of endangered species per plot included all species that are listed as endangered or vulnerable on the red list of the respective federal state of Germany where the grassland was located (BREUNIG & DEMUTH 1999, KORSCH & WESTHUS 2001, GARVE 2004, MIERWALD & ROHMAHN 2006, RISTOW et al. 2006, POPPENDIECK et al. 2010, RAABE et al. 2010). Furthermore, we calculated the Shannon diversity index and the evenness as additional diversity measures. Plant functional groups (percentage cover sums of grasses, legumes, non-legume herbs, shrubs and bryophytes) were calculated per plot to track differences in the functional composition and vegetation structure of differently managed grasslands.

To explore major floristic gradients independent of management schemes and their relation with environmental characteristics two *Detrended Correspondence Analyses* (DCAs) were performed using PC-ORD 5.1 (HILL & GAUCH 1980). DCAs were run using square-root transformed abundance data, excluding species present in less than eight plots and down-weighting of rare species The first ordination included all 202 plots. The distinct separation of the northern and northwestern regions from the others in this DCA (Supplement E1) pointed at strong regional peculiarities. Thus, a second DCA was run with the 149 plots of the northeastern, central and southwestern regions.

To test for significant differences in environmental and vegetation parameters among management schemes (year-round pasture, seasonal pasture, mown pasture, meadow with autumn or winter pasture, meadow), we calculated ANOVAs and subsequent Tukey tests for normal distributed variables with homogeneous variances. Data were treated with log or square-root transformations where necessary. Completely non-normal data were analyzed using Kruskal-Wallis H-tests with pairwise comparisons using Mann-Whitney U tests. Probability values from pairwise comparisons were adjusted using Holm correction. Multiple linear regression models were used to explain plant species richness, Shannon diversity and evenness. A generalized multiple linear model with Poisson error structure was applied to explain numbers of endangered species. Within these models, environmental indicator values (Ellenberg M, N, R), "mowing" as categorical variable for regularly mown grasslands such as mown pastures, meadows with and without autumn/winter grazing (49% of all plots), "grazing" as categorical variable for grazed grasslands such as year-round pastures, seasonal pastures, mown pastures and meadows with autumn/winter grazing (82% of all plots), "fertilization" (yes or no), and study regions were used as predictor variables. Each Ellenberg indicator value was represented by both linear and quadratic terms. Model assumptions were ensured by checking diagnostic plots. All statistical work except the DCA have been done with R 3.3.2 (R CORE TEAM 2016).

4. Results

4.1 Effects of management and soil characteristics on vegetation composition

Ordination analyses of all grassland plots revealed two major influential factors: management by year-round grazing and the study regions (Fig. 2, Supplement E1). Hence, grasslands from the regions Niederrhein-Westfalen and Friesland-Hamburg, in which most of the year-round pastures were sampled, were clearly separated from grasslands of the other three regions (Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb). Within the latter regions, only one grassland was a year-round pasture, but all others were seasonal pastures, mown pastures or meadows with or without winter grazing. These grasslands did barley show any pattern in the ordination space of all plots, except some slightly distinctly located seasonal pastures from the southwestern region at the upper end of the second axis (Fig. 2, Supplement E1). Even after removing year-round pastures and focusing on the plots of the three

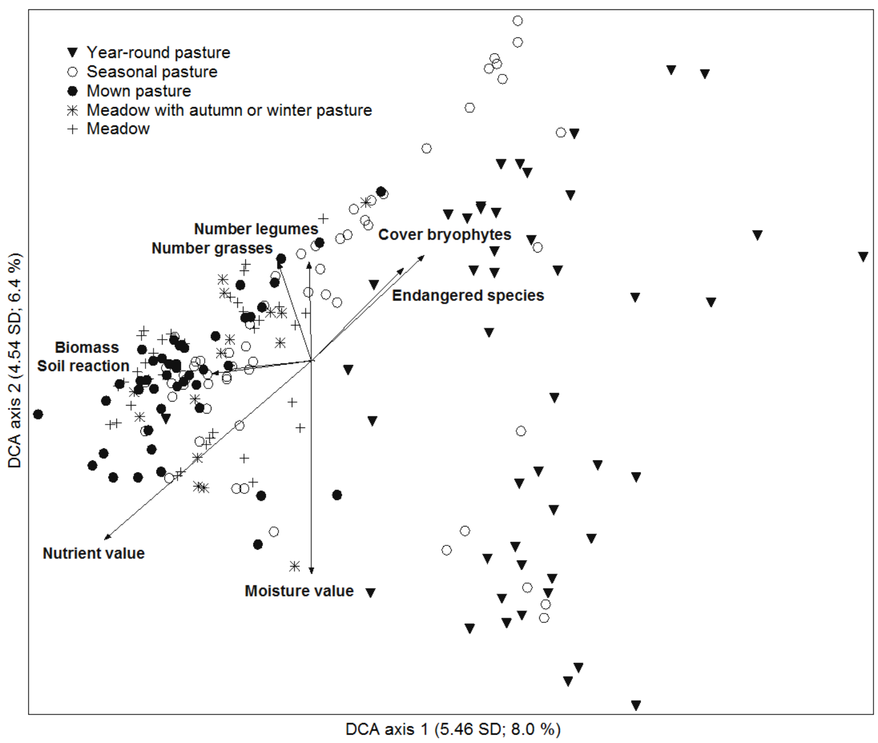

Fig. 2. DCA ordination diagramm of all plots categorized by management schemes with environmental vectors as overlay (n = 202). Total inertia: 6.59; for length of gradient and percentage of explained variance see axes titles.

Abb. 2. DCA Ordinationsdiagramm aller Untersuchunsgflächen eingeteilt nach Management-Typen mit nachträglicher Korrelation der Umweltvariablen (n = 202). Gesamtvarianz: 6,59; die Grandienten-länge und der Anteil der erklärten Gesamtvarianz ist den Achsenbeschriftungen zu entnehmen.

last mentioned regions, management schemes were only moderately separated (Fig. 3) and still a fractionation according to study region was visible (Supplement E2). Nevertheless, at least pure pastures and pure meadows were rather separated when focusing on three regions only. Generally, gradients of soil moisture, nutrient supply and productivity (aboveground biomass) were strongly related to vegetation composition (Fig. 2 and 3). These variables were largely negatively related with plant species richness, the number of endangered plant species and bryophyte cover. A gradient in soil reaction could be detected when all regions were analyzed together due to differences in bedrock and soil types among some of the regions (Table 1).

4.2 Differences among management schemes

Significant differences among management schemes were found for all recorded vegetation and environmental variables except for evenness and the cover of herbs (Table 3). While plant species richness and Shannon diversity were highest in seasonal pastures and lowest in year-round pastures, most endangered species were recorded in year-round pastures. Gener-

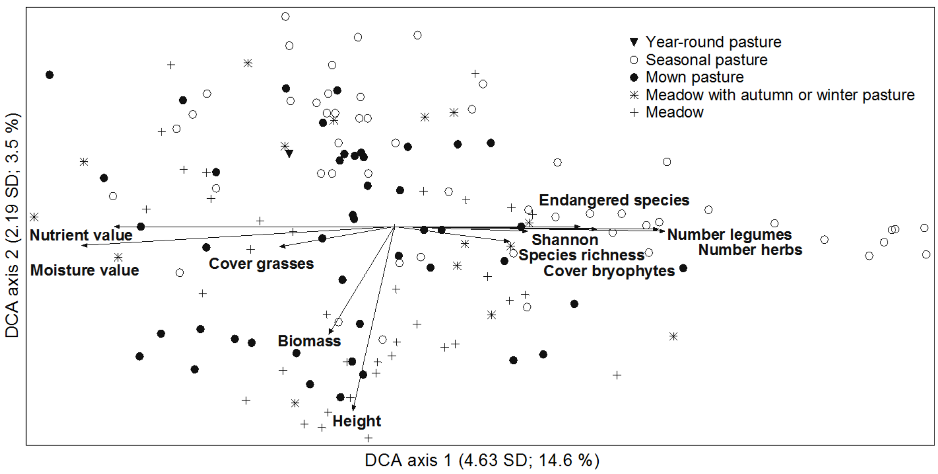

Fig. 3. DCA ordination diagramm of grasslands from the three study regions Schorfheide-Chorin (northeast), Hainich-Dün (central) and Schwäbische Alb (southwest) categorized by management schemes with environmental vectors as an overlay (*n* = 149). Total inertia: 3.63; for length of gradient and percentage of explained variance see axes titles.

Abb. 3. DCA Ordinationsdiagramm der Grünländer der Untersuchungsgebiete Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb eingeteilt nach Management-Typen mit nachträglicher Korrelation der Umweltvariablen (*n* = 149). Gesamtvarianz: 3,63; die Grandientenlänge und der Anteil der erklärten Gesamtvarianz ist den Achsenbeschriftungen zu entnehmen.

ally, lower numbers of plant species and endangered species were found in management schemes involving mowing (mown pastures and meadows with/without winter grazing), when compared to seasonal pastures. Within the schemes involving mowing, more than 50% of the grasslands (and up to 97% in case of meadows with autumn/winter grazing) were fertilized, whereas the vast majority of grazing-only systems was unfertilized. Thus, above-ground biomass production of schemes involving mowing was on average 55% higher compared with year-round and seasonal pastures. Year-round pastures exhibited lowest mean indicator values for soil reaction and nutrient supply, but with a large standard deviation indicating pronounced heterogeneity in environmental conditions. Cover values of bryophytes and shrubs as well as stand height were highest in year-round pastures compared to all other management schemes. In seasonal pastures nutrient values were similarly low as in year-round pastures and soil moisture as well as vegetation height were lowest compared to all other management schemes. Together with mown pastures, seasonal pastures had the highest cover values of legumes and bare soil. Grass cover, on the opposite, was highest in meadows without any grazing (Table 3).

4.3 Effects on plant diversity and endangered species

As stated above, plant diversity was strongly associated with environmental factors in ordination analyses (Fig. 2, Fig. 3). Regression models were calculated, to assess these highly influential factors in more detail. Management practice (fertilization, mowing, and grazing as categorical variables), environmental gradients (indicator values) and study regions explained in total from 26% (for evenness) to more than 60% (for species richness and num-

Table 3. Mean and standard deviation of diversity measures, vegetation composition and environmental indivcators for the different management schemes. Differences were tested by ANOVAs and subsequent Tukey tests when normal distribution and homogeneity of variance was given; otherwise by Kruskal-Wallis tests (KW) with multiple Mann-Whitney U tests (Holm corrected) as post-hoc tests. Significance levels: 0 < *** < 0.001 < ** < 0.01 < * < 0.05. Different letters indicate significant differences.

Tabelle 3. Mittelwerte und Standardabweichungen verschiedener Diversitätsmaße, der Vegetationszusammensetzung und der Zeigerwertewerte für die jeweiligen Grünland-Nutzungstypen. Unterschiede wurden mit ANOVAs und anschließenden Tukey-Tests getestet, wenn die Variablen normalverteilt und ihre Varianzen homogen waren; falls nicht, wurden Kruskal-Wallis-tests (KW) und Mann-Whitney U-Tests (mit Holm-Korrektur) gerechnet. Signifikanzniveaus: 0 < *** < 0,001 < ** < 0,01 < * < 0,05. Unterschiedliche Buchstaben symbolisieren signifikante Unterschiede.

		Year-round pasture	Seasonal pasture	Mown pasture	Meadow with autumn or winter pasture	Meadow
	Sign.	*n* = 46	*n* = 60	*n* = 45	*n* = 15	*n* = 36
Frequency of fertilized plots [%]		2	5	58	93	61
Species diversity						
Vascular plants/16 m^2	***	20.43 ± 7.12 c	34.18 ± 13.25 a	28.87 ± 8.92 ab	28.13 ± 7.68 ab	26.97 ± 7.56 b
Endangered species/16 m^2	***^{KW}	1.89 ± 2.15 a	1.58 ± 2.43 ab	0.22 ± 0.52 c	0.33 ± 0.62 bc	0.36 ± 0.83 c
Shannon index	***	1.85 ± 0.64 b	2.42 ± 0.5 a	2.19 ± 0.47 a	2.18 ± 0.38 ab	2.2 ± 0.45 ab
Evenness	n.s.	0.64 ± 0.18	0.71 ± 0.08	0.66 ± 0.11	0.65 ± 0.11	0.68 ± 0.11
Vegetation structure						
Biomass [g/m^2]	***	175.96 ± 139.92 b	193.03 ± 95.23 b	281.45 ± 90.66 a	243.35 ± 106.57 ab	326.15 ± 145.89 a
Vegetation height [cm]	***	36.57 ± 28.51 a	19.98 ± 18.37 b	29.44 ± 9.62 a	26.07 ± 7.36 ab	34.44 ± 11.85 a
Cover [%] of						
Bare soil	**	6.7 ± 11.96 ab	6.87 ± 11.78 a	6.14 ± 7.4 a	7.34 ± 8.45 ab	2.45 ± 5.5 b
Bryophytes	***	32.3 ± 31.62 a	17.99 ± 23.91 ab	7.53 ± 12.98 b	9.2 ± 12.27 ab	10.77 ± 19.91 b
Grasses	**	52.05 ± 33.81 b	48.82 ± 24.63 b	64.19 ± 26.1 a	53.93 ± 16.79 ab	71.11 ± 24.21 a
Legumes	**	7.15 ± 12.37 b	9.78 ± 11.45 a	13.98 ± 16.2 ab	4.55 ± 4.86 ab	5.11 ± 5.41 ab
Herbs	*[1]	61.41 ± 48.25	40.05 ± 25.46	28.62 ± 17.85	28.85 ± 23.67	27.12 ± 15.97
Shrubs	***^{KW}	7 ± 22.94 a	0.60 ± 3.26 ab	0.05 ± 0.11 bc	0.16 ± 0.25 abc	0.04 ± 0.17 c
Ellenberg values						
M (moisture)	**	5.7 ± 0.96 a	5.02 ± 0.79 b	5.37 ± 0.56 ab	5.47 ± 0.69 ab	5.49 ± 0.48 a
R (reaction)	***	5.28 ± 1.51 b	6.52 ± 0.69 a	6.4 ± 0.57 a	6.64 ± 0.45 a	6.45 ± 0.35 a
N (nutrients)	***	4.58 ± 1.59 c	5.29 ± 1.24 b	6.17 ± 0.78 a	5.99 ± 0.93 ab	6.14 ± 0.7 a

[1] Anova revealed significant differences, post-hoc test did not

Table 4. Statistics of the linear models for species richness, Shannon index, evenness and the generalized linear model for the number of endangered species (the latter with poisson error structure). Significance levels: 0 < *** < 0.001 < ** < 0.01 < * < 0.05. Each environmental indicator value entered the models as both linear and quadratic terms (^2). Variables for management (fertilization, grazing, mowing) are all categorical (yes vs. no). For the five study regions the estimate and significance of the least significant region is given. *n* = 202.

Tabelle 4. Ergebnisse der linearen Modelle berechnet für Artenzahl, Shannon-Index, Evenness, und des generalisierten linearen Modells für die Anzahl gefährdeter Arten (letzteres mit Poisson-Verteilung). Signifikanzniveaus: 0 < *** < 0,001 < ** < 0,01 < * < 0,05. Die Ellenberg-Zeigerwerte wurden sowohl linear als auch quadriert (^2) in das Modell aufgenommen. Alle Management-Varibalen (Düngung, Beweidung, Mahd) sind kategorial (ja vs. nein). Für die fünf Untersuchungsgebiete sind Estimate und Signifikanz der am wenigsten signifikanten Region angegeben. *n* = 202.

Response variable	**Species richness**		**Number of endangered species**		**Shannon index**		**Evenness**	
R^2	61%		64%		40%		26%	
Predictor variables	Estimate	Sign.	Estimate	Sign.	Estimate	Sign.	Estimate	Sign.
Ellenberg indicator values								
Moisture value	-1.55	*	-3.06	**	1.69	0.42	0.05	0.75
Moisture value^2	0.11	0.10	0.24	**	-0.17	0.35	-0.01	0.71
Reaction value	0.72	*	1.02	*	0.71	0.44	0.07	0.30
Reaction value^2	-0.06	0.06	-0.08	0.06	-0.01	0.86	-0.01	0.39
Nutrient value	0.95	**	0.72	0.09	2.73	***	0.26	***
Nutrient value^2	-0.10	***	-0.12	**	-0.30	***	-0.03	***
Management								
Fertilization (no)	0.45	***	0.79	*	0.25	0.50	-0.02	0.39
Grazing (yes)	0.00	1.00	0.16	0.65	0.51	0.19	0.03	0.36
Mowing (yes)	-0.19	0.18	-0.07	0.81	-0.68	0.09	-0.05	0.10
Study region	-0.94	***	-1.54	***	-2.13	***	-0.15	***

bers of endangered species) of the variance in the diversity data (Table 4). In line with the ordination analysis, all diversity measures were strongly negatively related to nutrient supply. However, a slight hump-shaped relation with a decrease of diversity at very low nutrient values below three could be detected (Fig. 4) and was also reflected by the significant effect of the quadratic term of the nutrient value in the regression model (Table 4). Both plant species richness and numbers of endangered species were negatively related to soil moisture and fertilization. Whereas plant diversity strictly increased with increasing soil reaction values, the number of endangered species exhibited two peaks, one at rather low soil reaction (Ellenberg R from 4 to 5) and one at highest values (Ellenberg R above 7; Fig. 4). Presence of mowing or grazing was not significantly related to any diversity measures, whereas the study region had a significant effect in all cases (Table 4).

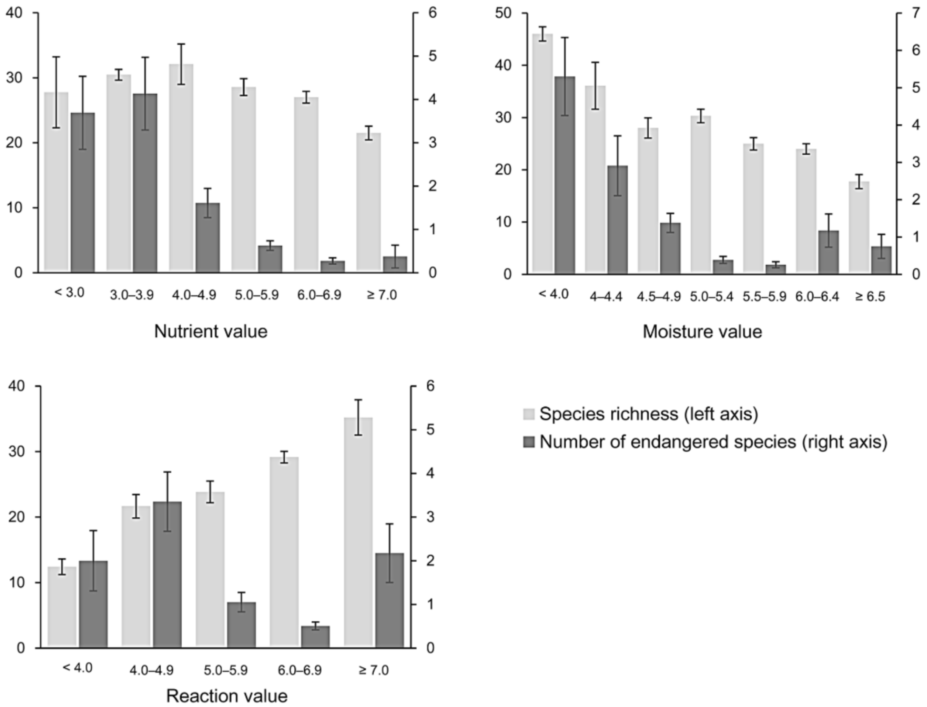

Fig. 4. Plant species richness and numbers of endangered species along gradients of nutrient supply, soil moisture and soil reaction according to Ellenberg indicator values (ELLENBERG et al. 2001). For each category of the indicator values, mean numbers of plant species and endangered species per plot are shown. All management schemes included.

Abb. 4. Pflanzenartenvielfalt und die Anzahl an gefährdeten Arten entlang der Gradienten von Nährstoffverfügbarkeit, Bodenfeuchte und Bodenreaktion nach Ellenberg Zeigerwerten (ELLENBERG et al. 2001). Jede Kategorie eines Zeigerwerts zeigt den Mittelwert von Pflanzenartenvielfalt und gefährdeten Arten pro Aufnahme. Alle Management-Typen einbezogen.

5. Discussion

5.1 Impact of management on vegetation composition, plant diversity and endangered species

Our study showed that plant functional group composition, plant diversity and endangered species occurrence significantly varied among management schemes (Table 3). On the one hand, meadows (also mown pastures and autumn/winter grazed meadows) had significantly higher productivity and grass cover but contained less (endangered) plant species when compared to seasonal pastures. This is at least partly the result of meadows being generally more intensively used with frequent fertilization, whereas many of the studied pure pastures were completely unfertilized, such as dry calcareous Mesobromion-communities (SOCHER et al. 2012). In terms of functional group and species composition meadows with autumn/winter grazing as well as mown pasture were somewhat similar to pure meadows, but had lower grass cover and higher proportions of bare soil, resulting from occasional grazing. Seasonal pasture, the most traditional land use in our study (POSCHLOD et al. 2009), contained most (endangered) plant species, although even within this management scheme diversity measures varied considerably. Due to a generally large variation within management types and a high temporal variability within sites (BLÜTHGEN et al. 2012, ALLAN et al. 2014), the composition of the vegetation did not reflect our predefined management schemes very well. For example, some mown pastures are grazed and mown within one year, but in other years they may be exclusively grazed or mown, resulting in a wide range of possible management effects on the vegetation. Thus, our study also implies that traditional categories of management schemes do often not fit today's situation.

Year-round pastures differed considerably from all other, more agriculturally oriented schemes, in that they were on average less species-rich but harboured highest mean numbers of endangered species. This seemingly contradiction is caused by the fact that year-round grazing is often used as a nature conservation tool for wide areas which encompass many (semi-)open habitats of different conservation value, where the traditional land use is economically not feasible, increasing the risk of abandonment and ongoing succession (RUPPRECHT et al. 2016, TÖRÖK et al. 2016). Thus, these habitat complexes contain (species-poor) late successional tall-herb and shrub formations, but also areas of short vegetation with high proportions of bare ground, where endangered species can successfully survive (GILHAUS et al. 2015). In our study, this is especially true for rare species of sandy, nutrient-poor and rather acidic grassland. Thus, our results also underline the successful maintenance of the high conservation value of such sites with year-round grazing (FELINKS et al. 2012, RUPPRECHT et al. 2016). Due to the clustered occurrence of year-round pastures in two study regions in the north and northwest of Germany (Table 2), which somewhat differed in environmental conditions from the other regions in having more sandy soils with low pH (Table 1), our results are not representative for year-round pastures per se. For example, KÖHLER et al. (2016) found year-round pastures located on calcareous soils being generally very species-rich. Due to the broad extent of our study, the five regions generally strongly influenced vegetation composition and diversity. Underlying factors at the regional scale might be a set of factors such as climate, geology, topography, nitrogen depositions, landscape-scale land-use intensity, but also land-use history and species pool (KLAUS et al. 2013b, LÜSCHER et al. 2015). Thus, a clear separation of management impacts from regional effects was difficult, especially for year-round pastures.

5.2 Mowing or grazing for grassland conservation?

Neither the presence of mowing nor grazing in grassland management turned out to be a significant predictor of plant diversity measures (Table 3). Thus, although management schemes significantly differed in diversity, neither mowing nor grazing can be generally recommended or generally non-recommended as best practice to conserve or promote plant diversity. This contrasts findings of other studies, where e.g., TÄLLE et al. (2016) found grazing to be more beneficial for the conservation value of grasslands compared to mowing. However, effects sizes found in this study were rather small and varied among grassland types (see below). A further reason for the rather indistinct pattern in our study may be that mowing and grazing were combined in many management schemes (BLÜTHGEN et al. 2012). This is further reinforced by the fact that almost all managements and management combinations additionally showed high temporal variability and inconsistency (ALLAN et al. 2014). Furthermore, sampled grasslands varied strongly in soil characteristics, vegetation types and the intensities of grazing and mowing, and the exact intensity of management such as the number of cuts and the type of livestock has not been assessed.

Nevertheless, grazing dominated schemes such as seasonal pastures turned out to be generally more species-rich than mowing dominated schemes such as meadows with or without winter grazing. However, even "ordinary" meadows with moderate diversity are endangered in many European countries today and thus worth being protected (BERG et al. 2014). Differences in plant diversity were also the result of inter-dependencies of management schemes with site-specific environmental conditions. For economic reasons more productive grasslands on deeper soils with better water supply are generally more intensively used and rather mown than grazed. This is in line with the studies of KLAUS et al. (2011) and SOCHER et al. (2012) showing a strong correlation between mowing frequency and fertilization intensity, which is known to be especially detrimental for plant diversity (ZECHMEISTER et al. 2003; Table 4). Thus, it is not solely the type of management (mowing or grazing), but the interplay of agricultural productivity potential and the intensity of land use which determine whether a managed grassland may harbour high species diversity or not. Sites which are less favourable for intensive use are often long lastingly managed by grazing without fertilization, sometimes since hundreds of years (POSCHLOD et al. 2009). For such grasslands, continuous grazing with a constant intensity level will be the best management option, while considerable changes in management will be detrimental, at least for the established plant community. However, other studies have shown that mowing can also be a suitable alternative to maintain grasslands of high conservation value (POPTCHEVA et al. 2009, TÄLLE et al. 2015, KRUSE et al. 2016), especially of wet meadows, which can be sensitive towards trampling when soils are water-saturated. For the conservation of many short-lived annual and biannual species, grazing is definitely the best option because it creates gaps of bare soil which are essentially needed as regeneration niches (FLEISCHER et al. 2013).

5.3 Effects of and interaction with environmental factors

Besides management and study regions, all recorded environmental variables impacted on the ecological value of the grasslands. Especially low nutrient supply but also rather dry conditions turned out to be beneficial for species diversity (Table 4). This is in line with previous studies, showing plant diversity to drastically decease at high productivity levels (e.g., GRACE 1999, ADLER et al. 2011, KLAUS et al. 2011). Although this relationship might not be strictly linear, our study contained only very few grasslands where low species richness was associated with low productivity (left side of hump-shaped curve as proposed by GRIME 1979). Whereas high plant species richness was clearly favoured by a moderate to high soil pH, highest numbers of endangered species occurred in grasslands on rather acidic soils (Fig. 4). These grasslands were low-productive sand grasslands and heathlands, where plants suffer from limited nutrient supply and drought. As biomass production is low under such rather extreme conditions, higher numbers of low-competitive specialist, which are nowadays often critically endangered, can occur (HAMMES et al. 2012, GILHAUS et al. 2015). A second, slightly lower peak of endangered species was found at high soil pH, as it is typical of rather shallow calcareous soils. Here, aboveground competition is also suppressed by limited nutrient-supply partly induced by drought which favours species-rich calcareous grasslands such as Mesobromion communities (DENGLER et al. 2014). Generally, our results point to the importance of the lower and upper end of the gradient of soil reaction, soil moisture and productivity as these sites often contained large numbers of endangered species at rather low-intensity of management, in particular grazing. In contrast, more productive grasslands of intermediate soil reaction and moisture conditions rarely harbour (endangered) specialist species as they are as a rule more intensively used. Thus, abiotic site conditions, regional species pools and site history may play a predominant role in shaping grassland diversity compared to the type of management by either grazing or mowing.

Erweiterte deutsche Zusammenfassung

Einleitung - Die meisten mitteleuropäischen Grünlandhabitate sind anthropogen entstanden und hängen von regelmäßiger Nutzung durch Mahd oder Beweidung ab (POSCHLOD et al. 2009). Seit der Intensivierung der Landwirtschaft in den 1950/60er Jahren ist artenreiches Grünland in Nordwest-Europa jedoch stark zurückgegangen, und wird deshalb heute vielerorts streng geschützt (WESCHE et al. 2012). Trotzdem hält europaweit der Trend der Nutzungsintensivierung und -änderung noch immer an (KÜMMERLE et al. 2016), sodass Studien zum Einfluss verschiedener Nutzungstypen auf die Artenvielfalt im Grünland wichtig für den Erhalt dieser Lebensräume sind. Generell wirken sich Beweidung und Mahd unterschiedlich auf die Vegetation aus, da Beweidung selektiv Pflanzen bzw. deren oberirdische Bestandteile schädigt, während Mahd alle Pflanzen einer Wiese in gleichem Maße betrifft (z. B. SOCHER et al. 2012, KLAUS et al. 2013a, b, BOCH et al. 2016, KRUSE et al. 2016). Die Bandbreite an Nutzungstypen und -intensitäten ist allerdings sehr groß und oft werden heutzutage Mahd und Beweidung auf einer Fläche kombiniert, weshalb auch die Einflüsse auf die Artvielfalt und die Artenzusammensetzung vielseitig sind (BLÜTHGEN et al. 2012). In dieser Studie untersuchen wir den Einfluss verschiedener Nutzungstypen (Ganzjahresweiden, Saisonweiden, Mähweiden, Wiesen mit Nachbeweidung im Herbst oder Winter und reine Wiesen) in Interaktion mit abiotischen Standortfaktoren auf die Vegetationszusammensetzung und deren Vielfalt in fünf Regionen Deutschlands.

Untersuchungsgebiete - Wir haben 202 Vegetationsaufnahmen in 169 unterschiedlich genutzten Grünlandflächen in fünf verschiedenen Regionen Deutschlands angefertigt: Friesland-Hamburg (Norden), Niederrhein-Westfalen (Nordwesten), Schorfheide-Chorin (Nordosten), Hainich-Dün (Mitte) und Schwäbische Alb (Südwesten), siehe auch Tabelle 1 und Abbildung 1. Die letztgenannten drei Regionen sind Teil des Forschungsprojekts „Biodiversitäts-Exploratorien" zur Erforschung funktionaler Zusammenhänge zwischen Artenvielfalt, Ökosystemfunktionen und Landnutzung (www.bioversity-exploratories.de; FISCHER et al. 2010). Während das Klima im Nordwesten Deutschlands ausgeprägt atlantisch ist, liegt den Untersuchungsgebieten ein klimatischer Gradient mit nach Nordosten zunehmender Kontinentalität zugrunde. Die Untersuchungsgebiete unterscheiden sich zudem hinsichtlich weiterer regionalen Gegebenheiten wie etwa Geologie und Boden (Tab. 1).

Material und Methoden - Unsere Studie beinhaltet sehr unterschiedliche Grünlandbestände (Tabelle 2). Das landwirtschaftliche Grünland konnte den folgenden pflanzensoziologsichen Verbänden zugeordnet werden: *Arrhenatherion elatioris* W. Koch 1926, *Bromion erecti* Koch 1926, *Cynosurion cristati* Tx. 1947 mit von Höhe, Topografie und Bodenfeuchte abhängigen Übergängen zu *Polygono-Trisetion* Br.-Bl. et Tx. ex Marschall 1947 nom. invers. propos., *Calthion* Tx. 1937 und *Magno-Caricion elatae* W. Koch 1926. Auf den zumeist sehr weitläufigen Ganzjahresweiden waren unterschiedliche Vegetationstypen auf einer Fläche vorhanden, die zu den Verbänden *Cynosurion cristati*, *Arrhenatherion elatioris*, *Arction lappae* Tx. 1937, *Calthion*, *Magno-Caricion elatae*, *Ericion tetralicis* Schwickerath 1933, *Genisto-Callunion* Böcher 1943, *Corynephorion canescentis* Klika 1931, *Koelerion arenariae* Tx. 1937 und *Thero-Airon* Tx. ex Oberdorfer 1957 gezählt werden konnten. Die untersuchten Grünlandflächen wurden in fünf verschiedene Nutzungstypen kategorisiert: Ganzjahresweiden, Saisonweiden (manchmal mit einem Mulchschnitt nach der Beweidung), Mähweiden (Mahd und Beweidung werden in etwa ähnlicher Intensität kombiniert), Wiesen mit Nachbeweidung im Herbst oder Winter und Wiesen (ausschließlich gemäht). Mit Ausnahme der Ganzjahresweiden liegen für jeden Nutzungstyp jeweils gedüngte und ungedüngte Flächen vor. Pro Grünlandfläche wurde in der Regel eine Aufnahmefläche angelegt, in sehr heterogenen und weitläufigen Beständen jedoch eine Aufnahmefläche pro Vegetationstyp, besonders in den Ganzjahresweiden. Pro Aufnahmefläche wurden die Artenzusammensetzung der Vegetation auf 4 m × 4 m, einige Strukturparamater und das jeweilige Management aufgenommen, sowie die oberirdische Pflanzenbiomasse beprobt. Für die Auswertung wurden zusätzlich mittlere Ellenberg-Zeigerwerte (ELLENBERG et al. 2001) und die Anzahl an Rote Liste-Arten pro Aufnahme berechnet (BREUNIG & DEMUTH 1999, KORSCH & WESTHUS 2001, GARVE 2004, MIERWALD & ROHMAHN 2006, RISTOW et al. 2006, POPPENDIECK et al. 2010, RAABE et al. 2010). Floristische Unterschiede der verschiedenen Nutzungstypen, aber auch der unterschiedlichen Regionen, wurden mit multivariaten Ordinationen untersucht (DCA). Unterschiede in der Vegetationsstruktur sowie in den weiteren Umweltparametern zwischen den Nutzungstypen wurden mittels Gruppenvergleichen auf Signifikanz getestet. Außerdem wurden Regressionsmodelle zur Erklärung von Artenzahl, Anzahl an Rote Liste-Arten, Shannon-Diversitätsindex und Evenness anhand von Nutzung und Standortfaktoren berechnet.

Ergebnisse - In der Artenzusammensetzung der Vegetation wichen besonders die Ganzjahresweiden deutlich von allen anders genutzten Grünländern ab, wohingegen die floristischen Unterschiede zwischen Saisonweiden, Mähweiden und Wiesen mit und ohne Nachbeweidung recht gering waren (Abb. 2, 3). Außerdem zeigte sich ein starker Einfluss der Region auf die floristische Zusammensetzung, der den Effekt der Nutzungstypen teilweise überlagerte (Anhang E1, E2). Die Vegetationszusammensetzung der Flächen wurde zudem deutlich von der Bodenfeuchte, der Nährstoffverfügbarkeit und der Produktivität der Standorte beeinflusst.

Darüber hinaus ergaben die Analysen, dass sich innerhalb einiger Nutzungstypen alle erhobenen Parameter bis auf die Evenness und die Deckung an Kräutern voneinander unterschieden (Tab. 3). Die höchste Zahl von Pflanzenarten wurde auf Saisonweiden gefunden, während die geringste Artenvielfalt im Mittel auf den Ganzjahresweiden festgestellt wurde. Diese wiesen jedoch hohe Werte bei der Anzahl der gefährdeten Arten auf (Tab. 3). Der Aufwuchs war auf den primär gemähten Wiesen und Mähweiden am höchsten, wobei viele dieser Flächen im Gegensatz zu den meisten Weiden auch gedüngt wurden (Tab. 3).

Alle Diversitätsmaße (Artenzahl, Anzahl an Rote Liste-Arten und Evenness) zeigten einen negativen Einfluss der Nährstoffverfügbarkeit (Tab. 4). Die Artenzahl und die Anzahl an gefährdeten Arten wurden außerdem negativ durch Bodenfeuchte und Düngung beeinflusst. Während die Artenzahl zudem mit dem Ellenberg R-Wert linear anstieg, war die Anzahl an gefährdeten Arten zum einen bei sehr niedrigen und zum anderen bei sehr hohen R-Werten am höchsten und bei mittleren R-Werten am geringsten (Abb. 4). Im Gegensatz zur Düngung zeigten Mahd und Beweidung als Managementfaktoren keinen statistisch signifikanten Einfluss auf die untersuchten Diversitätsmaße.

Diskussion - Die funktionale Zusammensetzung, die Diversität und die Anzahl gefährdeter Arten unterschied sich deutlich zwischen den verschiedenen Nutzungstypen. Die Artenzusammensetzung war allerdings auch sehr deutlich regionsspezifisch geprägt, was den großen Einfluss von Geologie, Klima, Artenpool, Nutzungsgeschichte usw. auf die Vegetation verdeutlicht (KLAUS et al. 2013b, LÜSCHER et al. 2015). Dennoch ließen sich Ganzjahresweiden floristisch klar von den anderen Nutzungstypen abgrenzen und wiesen zwar im Mittel am wenigsten Pflanzenarten, dafür aber eine sehr hohe Anzahl an gefährdeten Arten auf. Dieser scheinbare Gegensatz lässt sich vor allem damit erklären, dass Ganzjahresbeweidung meist aus Naturschutzgründen auf unproduktiven, oftmals bodensauren Sandstandorten durchgeführt wird, die für landwirtschaftliche Grünlandnutzung aus ökonomischen Gründen wenig geeignet sind (LORENZ et al. 2016, RUPPRECHT et al. 2016). Solche Grünlandkomplexe bestehen oft aus (artenarmen) Hochstauden-Fluren und Dominanzbeständen, aber auch aus Sandmagerrasen und Heide-Elementen, die trotz geringer Artenzahl besonders viele geschützte Arten beinhalten (GILHAUS et al. 2015). Allerdings müssen Ganzjahresweiden nicht per se artenarm sein, wie KÖHLER et al. (2016) für Bestände auf kalkhaltigen Böden gezeigt haben. Die geringe Artvielfalt der Ganzjahresweiden in unserer Studie ist somit auch damit zu begründen, dass gerade diese Flächen zumeist auf sauren, sandigen Substraten lagen.

Zudem unterschieden sich rein beweidete Grünländer (besonders Saisonweiden) in der Vegetation deutlich von Mähweiden und Wiesen mit und ohne Nachbeweidung, die eine höhere Deckung an Gräsern, eine höhere Produktivität und eine etwas geringere Artenzahl aufwiesen. Dies liegt wohl nicht ausschließlich an der Nutzung, sondern auch daran, dass auf den von uns untersuchten Flächen eine Mahd häufiger mit Düngung einherging als eine Weidenutzung. Diese Ergebnis zeigte sich auch in anderen Untersuchungen (KLAUS et al. 2011, SOCHER et al. 2012).

Vor allem ein niedriges Nährstoffniveau, eher trockenen Bodenverhältnisse und eine damit einhergehende geringe Produktivität wirkten sich positiv auf die Diversität aus. Dies ist in Übereinstimmung mit andern Studien (z.B. GRACE 1999, ADLER et al. 2011, KLAUS et al. 2011). Als Hotspots gefährdeter Arten fanden sich zum einen Grünländer saurer Standorte (Sandmagerrasen, Heiden) und zum anderen solche basischer Standorte (Kalkmagerrasen), die eine durch Trockenheit limitierte Nährstoffverfügbarkeit und damit geringere Konkurrenz zwischen den Pflanzenarten aufweisen (DENGLER et al. 2014).

Unsere Ergebnisse lassen zwar keine generelle Empfehlung für oder gegen Mahd oder Beweidung zum Erhalt von artenreichem Grünland zu, da weder Mahd noch Beweidung in den Regressionsmodellen als entscheidender Faktor identifiziert werden konnte, jedoch konnten wir deutlich zeigen, dass sich Düngung negativ auf die Diversität der Vegetation auswirkt. Da auf den untersuchten Flächen Mahd häufig mit Düngung gekoppelt war, waren die primär von Mahd geprägten Nutzungstypen weniger divers, als die größtenteils nicht gedüngten Saisonweiden. Dies trat auch in Studien von KLAUS et al. (2011) und SOCHER et al. (2012) auf, wobei Nutzungstyp und -intensität auch stark vom landwirtschaftlichen Potenzial der Flächen abhängig sind. Somit wirkt sich nicht nur der Nutzungstyp allein, sondern auch die daran gekoppelten Umweltbedingungen der Grünlandflächen auf die Diversität der Vegetation aus. Tiefgründige Böden werden beispielsweise oft intensiver genutzt als flachgründige. Unter extensiver Nutzung ohne Düngung kann sowohl durch Beweidung als auch Mahd artenreiches Grünland erhalten werden (POPTCHEVA et al. 2009, TÄLLE et al. 2015, KRUSE et al. 2016), wobei Beweidung oft verstärkt auf trockenen und Mahd verstärkt auf feuchteren Standort durchgeführt wird. Vorteilhaft für kleinwüchsige, annuelle Arten ist allerdings die Entstehung von Offenbodenstellen, was nur durch Beweidung und nicht durch Mahd erreicht werden kann (FLEISCHER et al. 2013). Unsere Studie hat auch gezeigt, dass moderne Grünlandnutzung nicht mehr einfach in die typischen Kategorien - Wiese, Weide, Mähweide – aufgeteilt werden kann, da viele Flächen gleichzeitig durch Mahd und Beweidung genutzt werden, und diese Nutzung zudem zeitlich sehr variabel ist (ALLAN et al. 2014).

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. DCA ordination diagramm of all plots categorized by study regions with environmental vectors as an overlay (*n* = 202).

Anhang E1. DCA Ordinationsdiagramm aller Untersuchungsflächen eingeteilt nach Untersuchungsgebieten mit nachträglicher Korrelation der Umweltvariablen (*n* = 202).

Supplement E2. DCA ordination diagramm of grasslands from the three study regions Schorfheide-Chorin (northeast), Hainich-Dün (central) and Schwäbische Alb (southwest) categorized by study regions with environmental vectors as an overlay (*n* = 148).

Anhang E2. DCA Ordinationsdiagramm der Grünländer der Untersuchungsgebiete Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb eingeteilt nach Untersuchungsgebieten mit nachträglicher Korrelation der Umweltvariablen (*n* = 148).

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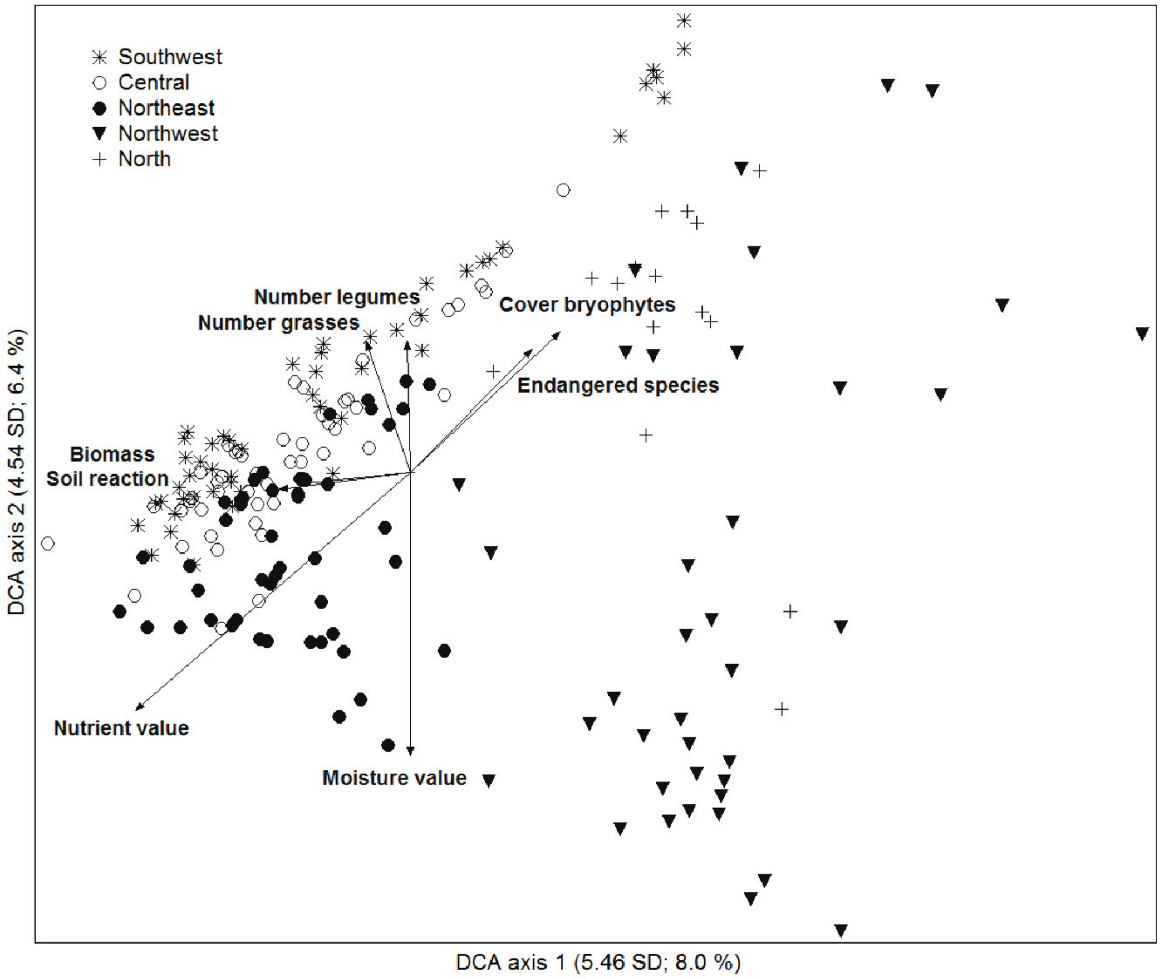
Supplement E1. DCA ordination diagramm of all plots categorized by study regions with environmental vectors as an overlay (n = 202). Total inertia: 6.59; for length of gradient and percentage of explained variance see axes titles.

Anhang E1. DCA Ordinationsdiagramm aller Untersuchungsflächen eingeteilt nach Untersuchungsgebieten mit nachträglicher Korrelation der Umweltvariablen (*n* = 202). Gesamtvarianz: 6.59; die Grandientenlänge und der Anteil der erklärten Gesamtvarianz ist den Achsenbeschriftungen zu entnehmen.



Supplement E2. DCA ordination diagramm of grasslands from the three study regions Schorfheide-Chorin (northeast), Hainich-Dün (central) and Schwäbische Alb (southwest) categorized by study regions with environmental vectors as an overlay (n = 148). Total inertia: 3.53; for length of gradient and percentage of explained variance see axes titles.

Anhang E2. DCA Ordinationsdiagramm der Grünländer der Untersuchungsgebiete Schorfheide-Chorin, Hainich-Dün and Schwäbische Alb eingeteilt nach Untersuchungsgebieten mit nachträglicher Korrelation der Umweltvariablen (n = 148). Gesamtvarianz: 3.63; die Grandientenlänge und der Anteil der erklärten Gesamtvarianz ist den Achsenbeschriftungen zu entnehmen.