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ORIGINAL PAPER

Local and landscape responses of biodiversity in calcareous grasslands

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Abstract

Across Europe, calcareous grasslands become increasingly fragmented and their quality deteriorates through abandonment and land use intensification, both affecting biodiversity. Here, we investigated local and landscape effects on diversity patterns of several taxonomic groups in a landscape of highly fragmented calcareous grassland remnants. We surveyed 31 grassland fragments near Göttingen, Germany, in spring and summer 2017 for vascular plants, butterflies and birds, with sampling effort adapted to fragment area. Through regression modelling, we tested relationships between species richness and fragment size (from 314 to 51,395 m^2), successional stage, habitat connectivity and the per cent cover of arable land in the landscape at several radii. We detected 283 plant species, 53 butterfly species and 70 bird species. Of these, 59 plant species, 19 butterfly species and 9 bird species were grassland specialists. Larger fragments supported twice the species richness of plants than small ones, and hosted more species of butterflies, but not of birds. Larger grassland fragments contained more grassland specialist plants, but not butterfly or bird specialists. Increasing amounts of arable land in the landscape from 20 to 90% was related to the loss of a third of species of plants, and less so, of butterflies, but not of birds. Per cent cover of arable land negatively correlated to richness of grassland specialist plants and butterflies, but positively to grassland specialist birds. We found no effect by successional stages and habitat connectivity. Our multi-taxa approach highlights the need for conservation management at the local scale, complemented by measures at the landscape scale.

Keywords Abandonment · Birds · Butterflies · Land use intensification · Nature conservation · Vascular plants

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Introduction

During the twentieth century, land use changes towards agricultural intensification or abandonment decreased biodiversity and fragmented and degraded semi-natural biotopes, such as grasslands, across Europe (Bauer and Albrecht 2020, Poschlod and Wallis de Vries 2002). Semi-natural grasslands comprise sown and non-sown rangelands that developed anthropogenically through extensive forms of livestock herding and/ or mowing (Poschlod and Bonn 1998, Wallis de Vries et al. 2002, Willems 2001). Grazing as well as clearing of shrubs and tree saplings on semi-natural grasslands is a fundamental disturbance that prevents succession to forests (Hansson and Fogelfors 2000), which is the climax ecosystem in many central European landscapes. However, decreases in economic viability of sheep, goat and cattle grazing for wool, milk and meat reduced the number of sheep kept in Germany from 30 million in 1860 to 1.57 million by 2018 (Eurostat 2019). The subsequent abandonment of land, in addition to land use changes and intensification diminished plant species richness (Jacquemyn et al. 2011) with negative cascading effects on other grassland species over the long term (Balmer and Erhardt 2000; Gossner et al. 2016; Haddad et al. 2009; Polus et al. 2007). Nowadays, the conservation of semi-natural grasslands through management or avoidance of intensification is of high priority in Europe (Kahmen et al. 2002; Poschlod and WallisDeVries 2002; Valkó et al. 2016).

Due to their extraordinary plant species richness with up to 40 species per m^2 (Ellenberg and Leuschner 2010) and their vast decline, calcareous grasslands are of particular conservation concern in Europe. They are listed in Annex I of the Natura 2000 Habitats Directive (92/43/EEC) and are endangered in Germany (Finck et al. 2017). Dry grasslands on calcareous soils are considered the most species-rich grasslands in Central Europe (Diekmann et al. 2014; Karlik and Poschlod 2009; WallisDeVries et al. 2002), holding the world record for vascular plant species richness at small scales (Wilson et al. 2012). Due to their nutrient-poor conditions on shallow soils, calcareous grasslands provide optimal grounds for many rare and endangered species (Leuschner and Ellenberg 2017). However, these conditions also make these ecosystems and their distinct species composition vulnerable to the effects of environmental degradation, for example through climate change (Basto et al. 2018), atmospheric nutrient deposition (Bobbink et al. 2010) and by changes in land management.

Semi-natural grasslands in central Europe decreased substantially during the last century, e.g. in some regions of Germany by up to 95% (Brückmann et al. 2010). In a Europe-wide study, per region 18–80% of calcareous grassland area present in the middle of the twentieth century has been lost, with a range between 0 and 99.8% of area loss per patch (Krauss et al. 2010). Similarly, connectivity of grasslands in some regions decreased by up to 90% (Cousins et al. 2007). The most recent estimate of the extent of calcareous grassland in Natura 2000 habitats with high orchid richness in Germany is 31,079 ha, scattered into 924 sites (Calaciura and Spinelli 2008). The small size of many of these grassland fragments (with many less than one hectare) exposes them to edge effects, succession through abandonment and reduced connectivity, which reduces their genetic diversity and ecological fitness (Matthies et al. 2004). Therefore, conservation management plays a crucial role in maintaining these fragments both as core habitats and as stepping stones in agricultural landscapes (Madeira et al. 2016).

Additionally, long-lasting flow-on effects from the use of agrochemicals (Evans and Sanderson 2018; Melts et al. 2018) and from atmospheric nitrogen deposition (Dupre et al. 2010; Field et al. 2014) put grassland species under pressure (Fischer and Stocklin 1997). Specialist species might be more affected than generalist species, as specialist species are in many cases mono- or oligophagous and therefore decline more dramatically than polyphagous species (Ernst et al. 2017; Steffan-Dewenter and Tscharntke 2000; Wenzel et al. 2006). Generalist species often have greater dispersal ability and larger landscape-wide population pools, which might increase success of survival in fragmented grassland landscapes (Riibak et al. 2015). Declines in species richness and changes in species composition towards biotic homogenisation (McKinney and Lockwood 1999) may affect the multiple ecosystem functions that grasslands provide (Allan et al. 2015; Diekmann et al. 2014; Huber et al. 2017). To this end, generalist species provide most functions, but specialist species can play an important role in complementing functions and maintaining the resilience of the ecosystem.

To understand the conservation value of these remaining grassland fragments, it is thus important to observe multiple species groups (Zulka et al. 2014) and account for the surrounding landscape structures at various spatial scales (Diacon-Bolli et al. 2012; Soderstrom et al. 2001). Such multileveled evidence on species richness and community composition contributes to informed management recommendations for this highly fragmented ecosystem. Here, we investigated how different taxonomic groups respond to size, habitat connectivity and landscape context of calcareous grassland fragments. For this purpose, we conducted a multi-taxa survey on plants, butterflies and birds in 31 calcareous grassland fragments near Göttingen, Lower Saxony in 2017. We selected these species groups because we expected them to react differently to environmental changes, and because they contain both specialist and generalist species that differ in abilities to disperse across the landscape (Dormann et al. 2007; Habel et al. 2016). We asked (i) which environmental variables influence local biodiversity patterns of plants, butterflies and birds?; and (ii) which spatial scale of landscape composition affects local biodiversity patterns?

Material and methods

Study site selection

We sampled 31 calcareous grassland fragments in the vicinity of Göttingen, Lower Saxony (Germany), which were subject to earlier studies (Steffan-Dewenter and Tscharntke 2000; Krauss et al. 2003a, 2004). These sites represent a gradient in size and habitat connectivity and provide a sub-sample of a total of 285 calcareous grassland fragments in the landscape. The nearest distance of the 31 fragments to other calcareous grassland fragments was 55 m, the furthest distance was 1894 m. Management on the sites varied from no visible management actions to grazing with cattle, goats or donkeys. Mowing regime varied from one mowing event per year up to mowing twice per year. The calcareous grasslands belonged to the plant association *Gentiano-Koelerietum* (Krauss et al. 2003a, 2004), but succession towards the natural climax state of a woody vegetation community had completely transformed one of the small grassland patches into a young forest, while only two grassland patches showed no sign of succession taking place. Those two intact grassland patches were small and medium in size. The other 28 grassland patches showed natural succession taking place at least to some extent (Fig. 1).

Fig. 1 Location of the study area within Europe (inset map) and display of the 31 study sites near Göttingen (center of map), lower Saxony, Germany. Map data © ESRI, accessed through QGIS 3

Biodiversity sampling

On all 31 study sites, we conducted surveys of plants, butterflies and birds during spring and summer of 2017. We used an area-adapted sampling strategy similar to previous surveys in the years 1996 and 2000 for vegetation and butterflies (Krauss et al. 2003a, 2004).

Plant surveys

We surveyed vascular plants on two occasions in May/June and in August in a total of 188 5 m × 5 m quadrats. We adjusted the sampling effort to the size of the study site and thus placed one plot on small sites (314–1326 m^2), two plots on medium sites (1914–7887 m^2) and three plots on large sites (11,528–51,395 m^2) in each sampling round. In each quadrat, we recorded per cent cover of each vascular plant species. Additionally, we surveyed the grassland fragments for further vascular plant species occurring outside the plots. In the field, species were identified with Jäger (2011) and Jäger et al. (2013). Nomenclature followed GermanSL Version 1.3 (Jansen and Dengler 2008). We classified grassland specialist plant species following von Drachenfels (2016).

Butterfly surveys

We surveyed butterflies and burnet moths along a total of 155 timed transects between May and August on five occasions with an interval of approximately two weeks. We adapted the survey effort to the size of the study sites (Krauss et al. 2003a, b; Steffan-Dewenter and Tscharntke 2000). Transect time per walk was 20 min for small grasslands, 40 min for intermediate grasslands and 60 min for large grasslands. We conducted the surveys under suitable conditions (no rain, < 90% cloud cover, > 17 °C if clouded, > 13 °C if sunny, no strong wind (Pollard 1977)). Species identification and nomenclature followed Settele et al. (2015) for diurnal butterflies, and Zub (1996) and Weidemann and Köhler (1996) for burnets. Species that could not be distinguished with the help of external characteristics were counted as species-complex. We defined butterflies as grassland specialists when their known occurrence is linked to open, nutrient poor grassland habitats (Bink 1992) such as calcareous grasslands in Lower Saxony.

Bird surveys

We sampled birds through point counts (Bibby et al. 2000) between March and June 2017, following Südbeck and Weick (2005). We sampled each site on four different occasions throughout the season with a minimum interval of 10 days between the counts. During a 10-min survey sequence, we recorded all birds heard or seen within a fixed radius of 50 m around the centroid of the study site. Surveys began shortly after sunrise and ended at 10 am by the latest. We classified species as forest or open land species by using habitat categories of the Red List (Krüger and Nipkow 2015; Storchová and Hořák 2018).

Environmental variables

For subsequent analyses of biodiversity patterns, we used the following environmental variables as predictors: The current size of the fragments ("Fragment size") was calculated by a combined approach through observations in the field using a handheld GPS, which were then digitized and analyzed based on latest Google Earth satellite imagery in ArcGIS 10.4. Remnants were categorized into small (n = 11; 314–1326 m^2), medium (n = 12; 1914–7887 m^2) and large (n = 8; 11,528–51,395 m^2) sites based on Krauss et al. (2003a, b). A habitat isolation index I had been calculated for the study sites in the year 2000 with the following formula derived from Hanski et al. (1994):

$$I = \sum e^{-dij} A_j$$

with A_j as the size of the nearest calcareous grassland patch, and dij as distance to the study site i (Steffan-Dewenter and Tscharntke 2000). The index I served as a negative proxy for habitat connectivity ("Connectivity"). We calculated the per cent cover of arable land cover ("% arable") at different spatial scales around the centroid of the focal grassland fragments in buffers of 250 m steps from 250 to 3000 m based on ATKIS Data (LGLN 2017). Moreover, we estimated the stage of succession on a categorical scale from 1 (no succession) to 4 (transformed into a different ecosystem—young forest).

Statistical analysis

We calculated biodiversity patterns of all investigated taxonomic groups as a response to the above-mentioned environmental variables. For this, we estimated species richness for all taxonomic groups using Chao 1 estimator of asymptotic richness (Chao 1984) (function "estimateR"). Estimated species richness strongly correlated with observed species richness ($r = 0.93$ for plants, $r = 0.81$ for butterflies and $r = 0.57$ for birds). Estimated species richness served as the response variable in generalised linear models with Poisson error distribution in which the natural logarithm of the current size of grassland fragments, habitat connectivity and per cent cover of arable land at different spatial scales served as explanatory variables. We tested all environmental variables for collinearity in advance, with the highest correlation between fragment size and connectivity (Pearson´s r: 0.29). We created individual models for each taxon at each spatial scale and compared model performance by Akaike's Information Criterion (AIC). We also calculated generalised linear models with the number of grassland species per taxon as a response variable, using the same environmental explanatory variables. Through multivariate statistics, we investigated species composition per size class of each taxon with NMDS. For each ordination, we superimposed all environmental variables and tested for significant ($p < 0.05$) correlations on species composition (function "envfit"). All analyses were conducted using the package "vegan" (Oksanen et al. 2018) in the program R (R Core Team 2016).

Results

General findings

In total, we found 283 plant species, 53 butterfly species and 70 bird species. Of these, we identified 59 plant species, 19 butterfly species and 9 bird species as grassland specialists.

Local and landscape effects on different species groups

Species richness models

Our models revealed that species richness of plants significantly increased with increasing size of the grassland fragment (Table 1, Fig. 2a), while an increasing per cent cover of arable land up to a radius of 1500 m around the grassland fragment had significantly decreased plant species richness (Table 1, Fig. 2b). Butterfly species richness significantly decreased with an increasing amount of arable land at small spatial scales up to 1000 m. None of our models explained the estimated richness of birds on calcareous grassland fragments at any spatial scale. Neither landscape connectivity nor the successional stages were significant for our models on any investigated species group at any scale.

Grassland specialist models

Fragment size was a positive predictor for species richness of grassland specialist plants at all spatial scales (Table 2). The increasing per cent cover of arable land showed a significant decrease of grassland specialist plants at scales from 500 to 2250 m and for birds from 1000 to 1500 m.

Species composition

Across all taxonomic groups, there was more variability in the composition of small fragments (Fig. 3). Large and small fragments differed in their species composition most

Table 1 Results of the generalized linear mixed models for the estimated species richness of three different taxonomic groups at different spatial scales

	Radius (m)											
	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000
Plants												
AIC	*279.64*	*272.21*	***271.03***	*274.88*	*277.51*	*279.31*	*281.10*	*282.40*	*283.01*	*283.28*	*283.66*	*284.09*
Intercept	139.19***	141.00***	139.80***	139.86***	139.43***	137.53***	135.07***	132.83***	131.38***	130.92***	130.02***	128.14***
Fragment size	0.0005	0.0006*	0.0007*	0.0006*	0.0006*	0.0006*	0.0006*	0.0006*	0.0006*	0.0006*	0.0006	0.0006
Succession	− 7.96	− 2.66	− 2.25	− 4.74	− 6.10	− 6.64	− 7.22	− 7.90	− 8.19	− 8.37	− 8.77	− 9.37
Connectivity	− 0.0001	− 0.0001	− 0.0001	− 0.0001	− 0.0002	− 0.0002	− 0.0003	− 0.0003	− 0.0003	− 0.0003	− 0.0003	− 0.0003
% arable	− 0.45*	− 0.74**	− 0.78***	− 0.68**	− 0.60*	− 0.53*	− 0.44	− 0.35	− 0.31	− 0.29	− 0.25	− 0.18
Butterflies												
AIC	***212.46***	*215.31*	*216.72*	*216.93*	*217.68*	*218.75*	*219.35*	*219.54*	*219.72*	*219.74*	*219.76*	*219.60*
Intercept	45.43***	42.54***	41.58***	42.11***	42.31***	41.76***	41.42***	41.37***	41.26***	41.40***	41.64***	42.01***
Fragment size	0.00015	0.00022*	0.00023*	0.00022*	0.00022*	0.00022*	0.00023*	0.00023*	0.00023*	0.00023*	0.00024*	0.00024*
Succession	− 2.96	− 2.05	− 2.25	− 2.67	− 2.96	− 3.11	− 3.17	− 3.20	− 3.16	− 3.14	− 3.14	− 3.10
Connectivity	0.00001	− 0.00001	− 0.00002	− 0.00003	− 0.00005	− 0.00006	− 0.00006	− 0.00007	− 0.00006	− 0.00006	− 0.00006	− 0.00005
% arable	− 0.23**	− 0.21*	− 0.19*	− 0.19*	− 0.18	− 0.16	− 0.15	− 0.14	− 0.14	− 0.15	− 0.15	− 0.17
Birds												
AIC	*246.32*	*246.39*	*246.28*	*245.76*	*244.81*	*243.57*	*242.92*	***242.42***	*242.43*	*242.82*	*243.12*	*243.38*
Intercept	23.22*	21.13*	20.74*	19.26	17.41	15.97	15.31	14.74	14.70	14.75	14.59	14.48
Fragment size	− 0.00007	− 0.00006	− 0.00007	− 0.00007	− 0.00007	− 0.00009	− 0.0001	− 0.0001	− 0.00011	− 0.00011	− 0.00011	− 0.00011
Succession	− 1.13	− 1.68	− 1.92	− 2.29	− 2.62	− 3.04	− 3.29	− 3.44	− 3.57	− 3.53	− 3.44	− 3.36

Table 1 (continued)

	Radius (m)											
	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000
Connectivity	0.00016	0.00013	0.00012	0.00011	0.0001	0.0001	0.00011	0.0001	0.0001	0.00009	0.00009	0.00009
% arable	− 0.04	0.03	0.05	0.11	0.16	0.22	0.24	0.26	0.27	0.27	0.27	0.27

Model performance is compared by Akaike's information criterion (AIC, represented in italic), with the best performing model indicated in bold italics letters. Cell contain estimates of the explanatory variable. Significances of the explanatory variables are displayed by ***P < 0.001; **P < 0.01; *P < 0.05

prominently for plants and butterflies, while large and small sites shared species composition for birds (Fig. 3). The community composition of plants and butterflies was significantly related to the percent cover of arable land at 250 m radius around the grassland fragment and to the successional stage of the grassland fragment. The amount of arable land in the landscape correlated with plant species composition also at a radius of 1750 m. Patch size emerged as predictor for species composition of birds, but was only marginally significant for butterflies (Table 3). Neither habitat connectivity nor the per cent of arable land at a 3000 m radius around the grassland fragments in the landscape influenced species composition.

Discussion

Our study shows the diverging importance of several environmental variables for diversity in three taxonomic groups both at the local and at the landscape scale. At the local scale, the size of the calcareous grassland fragment predicted species richness of plants and butterflies, both for all species and for specialist species. In contrast, species richness of various taxonomic groups was independent of current habitat area in other studies (Deák et al. 2016; Huber et al. 2017; Lengyel et al. 2016), which is counterintuitive to the often-confirmed expectation that larger habitat area increases species richness (Adriaens et al. 2006; Cousins et al. 2007; Krauss et al. 2004). The per cent cover of arable land was far more important for species richness and species composition of plants and butterflies than connectivity to other dry grassland patches. These findings emphasize the hostility of landscapes that are dominated by intensive and homogenous cropland for species richness (Hallmann et al. 2017; Kormann et al. 2015). However, this effect was not pronounced for birds, which might be less sensitive to landscape connectivity and might be more tied to the presence of woody vegetation because of their higher mobility (Duflot et al. 2018; Dorresteijn et al. 2018).

Our results also concur with previous studies that documented the relatively low importance of connectivity (Adriaens et al. 2006; Cousins et al. 2007; Huber et al. 2017), despite its often-demonstrated importance for the immigration of new species and individuals (Rösch et al. 2015). Thus, it remains a challenge to derive general assumptions on the role of habitat connectivity (Ibáñez et al. 2014), as different taxonomic groups may respond differently to variables on the landscape scale (Lengyel et al. 2016). Considerations of both habitat area and connectivity, as well as landscape composition and configuration, can be important for explaining species diversity patterns (Lindgren and Cousins 2017). The per cent cover of arable land negatively affected both the species richness of all plants and butterflies as well as grassland specialist plants and butterflies. Moreover, the per cent cover of arable land influenced the species composition of all investigated taxonomic groups (supporting Kormann et al. 2015). Biodiversity management, thus, would ideally target both the local and the landscape scale (Loos et al. 2019). As an example, the introduction of buffer zones might prove beneficial for invertebrates (Madeira et al. 2016). Moreover, a closer examination of management details over long periods might provide more insights into the effect of quality of the calcareous grassland fragments on biodiversity.

Our study also observed one complete loss and decrease in size of some fragments. This observation is alarming as it highlights general trend of habitat loss in agricultural landscapes despite formal protection under Annex I of the EU habitats directive across EU member states (Calaciura and Spinelli 2008). The observed losses stem from abandonment

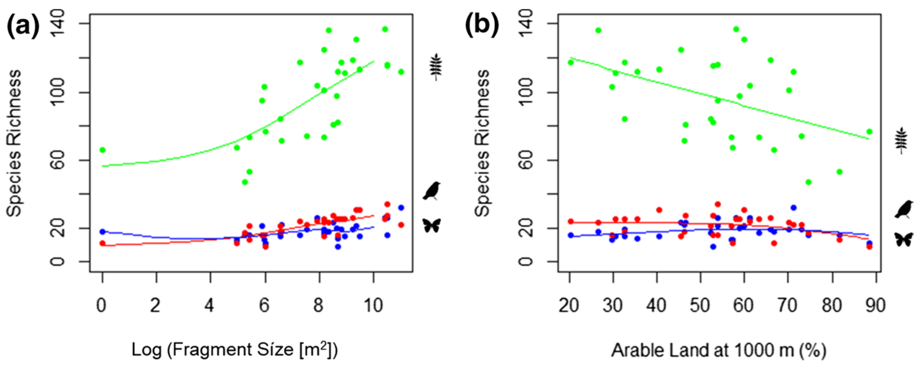

Fig. 2 Display of species richness for plants, butterflies, birds and **a** fragment size (natural logarithm); **b** per cent cover of arable land at 1000 m radius. Color code: plants = green, butterflies = red, birds = blue

and consequent succession on the one hand and transformation of land use, especially to margins of roads or to agricultural fields, on the other hand. At first, these small losses may appear insignificant, but in sum they constitute habitat loss at a larger scale. Such gradual changes are difficult to track and control, as the study area hosts almost 300 single fragments, of which approximately 70% are smaller than 1 ha (Rösch et al. 2015). The small size of these fragments and their isolated position in the landscape make it difficult and costly to maintain them (Gustavsson et al. 2007). No-action, however, poses a particular problem to calcareous grasslands, as they are naturally subject to succession. To halt this trend requires a lot of effort, particularly with the limited resources that are available at the implementing agency for nature conservation. Thus, prioritization of conservation efforts is necessary.

Whether it is more useful for conservation success to concentrate and improve the conservation value on few large sites or on many small sites is an old debate (e.g. Diamond 1975), which the responsible government authority alone cannot solve. From an ecological perspective, it has been shown that both small and large fragments are important for biodiversity at the landscape scale (Rösch et al. 2015; Tscharntke et al. 2002), as they play an important function as stepping stones (Lindborg et al. 2014; Wenzel et al. 2006) and create higher connectivity, which is a key factor for many ecological functions (Brückmann et al. 2010; Lindborg et al. 2014). Moreover, diverse landscapes are able to host higher species diversity (Mallinger et al. 2016). Thus, both large and small fragments are important to create a network of grassland patches (Deák et al. 2016; Rösch et al. 2015; Zulka et al. 2014). Nevertheless, maintenance of many small sites is linked to the practical challenge of affordable management regimes in the respective sites, which is key for their conservation (Huber et al. 2017).

For the conservation management of small grassland fragments, it might be useful to foster systematic collaborations with amateur animal keepers that use the grassland fragments for grazing of their horses (Köhler et al. 2016), donkeys, or small flocks of sheep, which through a rotational system might even promote seed dispersal between sites (Riibak et al. 2015). However, the type and stocking density of animals (Lyons et al. 2018, 2017), as well as the timing and duration of grazing affects calcareous grasslands differently (Goodenough and Sharp 2016; Römermann et al. 2009) and should thus be agreed upon and controlled. A viable alternative to grazing is mowing (Kahmen et al. 2002), even though mowing allows fewer seeds to be dispersed (Poschlod and Bonn 1998). Periodic

Table 2 Results of the generalised linear mixed models for the species richness of grassland specialist species of the three different taxonomic groups at different spatial Scales

	Radius (m)											
	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000
Grassland												
AIC	*215.79*	*209.59*	*205.39*	***205.21***	*206.13*	*207.58*	*209.91*	*213.29*	*215.29*	216.13	217.21	218.19
Intercept	41.15***	41.59***	41.74***	42.72***	43.38***	43.14***	42.60***	41.65***	40.85***	40.63***	40.27***	39.73***
Fragment size	0.00026*	0.00032**	0.00034***	0.00032***	0.00032***	0.00033***	0.00034**	0.00034**	0.00034**	0.00034**	0.00033**	0.00033**
Succession	−2.01	−0.25	0.18	−0.40	−0.75	−0.82	−0.90	−1.19	−1.34	−1.43	−1.63	−1.84
Connectivity	0	0.00002	0.00002	0.00001	0	−0.00002	−0.00003	−0.00004	−0.00004	−0.00004	−0.00003	−0.00004
% arable	−0.16	−0.25**	−0.29***	−0.29***	−0.29***	−0.28**	−0.26**	−0.22*	−0.20*	−0.19	−0.18	−0.15
Grassland butterflies												
AIC	*143.71*	*142.78*	*142.56*	*141.74*	***141.38***	*141.6*	*142.49*	*143.96*	*144.61*	144.72	145	145.27
Intercept	6.58**	6.49**	6.43**	6.69**	6.89***	6.87***	6.72**	6.41**	6.19**	*6.17***	*6.06***	*5.87***
Fragment size	0	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Succession	−0.8229	−0.5741	−0.5519	−0.5902	−0.6199	−0.6256	-0.6549	-0.7506	-0.8021	-0.8106	-0.8537	-0.9143
Connectivity	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
% arable	−0.03	−0.04	−0.04	−0.05	−0.05	−0.05	−0.04	−0.03	−0.02	−0.02	−0.02	−0.01
Grassland birds												
AIC	*87.86*	*86.7*	*85.66*	*83.93*	***83.87***	*84.52*	*85.01*	*85.56*	*86.34*	87.17	87.76	88.11
Intercept	0.86	0.88	0.86	0.71	0.64	0.67	0.69	0.71	0.76	0.81	0.85	0.87
Fragment size	0.00002	0.00002	0.00002	0.00002	0.00002	0.00002	0.00001	0.00001	0.00001	0.00001	0.00001	0.00002
Succession	−0.35	−0.46	−0.49	−0.48	−0.46	−0.45	−0.45	−0.44	−0.44	-0.42	-0.40	-0.39

Table 2 (continued)

	Radius (m)											
	250	500	750	1000	1250	1500	1750	2000	2250	2500	2750	3000
Connectivity	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001	0.00001
% arable	0.01	0.02	0.02	0.02*	0.02*	0.02*	0.02	0.02	0.02	0.02	0.02	0.01

Model performance is compared by Akaike's information criterion (AIC, represented in italics), with the best performing model indicated in Bold italics letters. Cell contain estimates of the explanatory variable. Significances of the explanatory variables are displayed by ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$

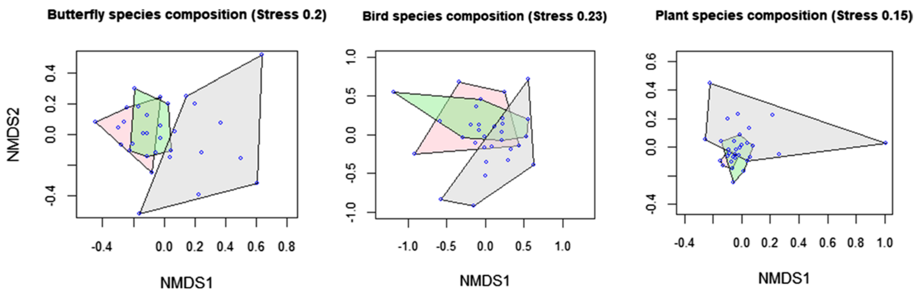

Fig. 3 Non-metric multi-dimensional scaling (NMDS) ordinations of species compositions in the three different taxonomic groups. Displayed are the first two axes of the ordination, with NMDS Axis 1 at the x axis and NMDS Axis 2 at the y axis, respectively. Blue dots indicate sites, Ordihull areas indicate size classes: grey = small, green = medium, pink = large

Table 3 Influence of environmental variables on species composition

	Plants	Butterflies	Birds
Patch size	0.113	0.069	0.039*
Connectivity	0.474	0.222	0.718
% Arable land 250 m	0.005**	0.022*	0.131
% Arable land 1750 m	0.032*	0.377	0.520
% Arable land 3000 m	0.311	0.987	0.930
Successional stage	0.006**	0.017*	0.932

Displayed are P-values of environmental variables from an environmental Fit function onto an ordination space of species composition for each respective taxon. *** < 0.001; ** < 0.01; * < 0.05; < 0.1; *n.s.* not significant

mowing, for example once in three years, seems helpful for the maintenance of species richness, as this intervention is able to avert the process of natural succession and is able to prevent vegetation change (Hansson and Fogelfors 2000). In general, a more diversified grassland management towards less intensity is favorable for semi-natural elements in the landscape (Diekmann et al. 2014; Gustavsson et al. 2007). Given the challenging conditions to translate diversification into practice, stewardship approaches and increased involvement of local people might pose a viable alternative to the bureaucratic formal options that agri-environmental schemes have offered so far.

Conclusion

Calcareous grasslands are facing serious conservation concerns, and the status of these habitats in Germany depends on many small-scale interventions to maintain their connectivity and quality. In particular, small grassland fragments (< 1.5 ha) are prone to shrub encroachment due to abandonment. Both local and landscape variables showed some impact on species richness and composition of some taxonomic groups, in particularly on habitat specialists. Given the difficulties to manage the many scattered fragments and the diverse conservation targets within the landscapes, novel and less formal approaches of maintenance of calcareous grassland might prove beneficial for conservation in the future.

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Declarations

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