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RESEARCH ARTICLE

Functional rather than structural connectivity explains grassland plant diversity patterns following landscape scale habitat loss

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Abstract

Context Functional connectivity is vital for plant species dispersal, but little is known about how habitat loss and the presence of green infrastructure interact to affect both functional and structural connectivity, and the impacts of each on species groups.

Objectives We investigate how changes in the spatial configuration of species-rich grasslands and related green infrastructure such as road verges, hedgerows and forest borders in three European countries have influenced landscape connectivity, and the effects on grassland plant biodiversity.

Methods We mapped past and present land use for 36 landscapes in Belgium, Germany and Sweden, to estimate connectivity based on simple habitat spatial configuration (structural connectivity) and accounting for effective dispersal and establishment (functional connectivity) around focal grasslands. We used the resulting measures of landscape change to interpret patterns in plant communities.

Results Increased presence of landscape connecting elements could not compensate for large scale losses of grassland area resulting in substantial declines in structural and functional connectivity. Generalist

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species were negatively affected by connectivity, and responded most strongly to structural connectivity, while functional connectivity determined the occurrence of grassland specialists in focal grasslands. Restored patches had more generalist species, and a lower density of grassland specialist species than ancient patches.

Conclusions Protecting both species rich grasslands and dispersal pathways within landscapes is essential for maintaining grassland biodiversity. Our results show that increases in green infrastructure have not been sufficient to offset loss of semi-natural habitat, and that landscape links must be functionally effective in order to contribute to grassland diversity.

Keywords Functional connectivity · Grassland · Biodiversity · Habitat loss · Habitat fragmentation · Land use change

Introduction

Habitat loss due to land use change is a key driver of global plant biodiversity declines (Foley et al. 2005; Newbold et al. 2015; Auffret et al. 2018). Grassland communities are particularly threatened because their high biodiversity depends on increasingly rare grazing management, along with high connectivity (Wilson et al. 2012; Cousins et al. 2015; Plue and Cousins 2018). Much of Europe has experienced an ongoing loss of species-rich grasslands over the last century, with many actively afforested, converted to arable land or intensive grassland, or abandoned to passively become forest (Eriksson et al. 2002; WallisDeVries et al. 2002; Kuemmerle et al. 2016; Watson et al. 2016). This habitat loss often leads to a decline in landscape connectivity for grassland plants (Hooftman and Bullock 2012; Auffret et al. 2015; Cousins et al. 2015).

Loss of landscape connectivity, i.e. reductions in the extent to which the landscape facilitates the movement of species (Taylor et al. 1993; Auffret et al. 2017) threatens grassland biodiversity, since plant populations in small grassland fragments are less likely to be rescued from local extinction through immigration from neighbouring populations (Eriksson 1996; Evju et al. 2015; Hooftman et al. 2015; Aguilar et al. 2019; Damschen et al. 2019). This is particularly the case for species with low dispersal capability and in sites which are no longer rotationally grazed by animals moving between habitat areas (Römermann et al. 2008; Ozinga et al. 2009; Schleicher et al. 2011; Plue et al. 2019). Declines in connectivity may also reduce our ability to restore species-rich grasslands on former agricultural or abandoned areas. Restored grasslands recover biodiversity more quickly when more species are present within the wider landscape, and when the sites are well-connected to other grassland habitats (Poschlod et al. 1998; Fagan et al. 2008; Piqueray et al. 2011, 2015; Winsa et al. 2015; Waldén et al. 2017).

Landscape connectivity is typically considered in terms of the physical amount and spatial distribution of suitable habitat, i.e. the structural connectivity (Haddad et al. 2015; McGuire et al. 2016). However, the functional connectivity of a landscape may be more ecologically meaningful, as it represents the ability of species to disperse effectively among habitat patches (Auffret et al. 2017). Functional connectivity is highly dependent upon structural connectivity, but also encompasses the ability of plant species to move among, and successfully establish within, suitable patches. Hence, it is also determined by the quality of available habitat and the behaviour and abundance of important biotic dispersal vectors such as birds, humans, or grazing livestock (Tischendorf and Fahrig 2000; Auffret et al. 2017). As well as declines in structural connectivity through direct habitat loss, land use intensification and the abandonment of traditional rotational grazing networks has likely further disrupted grassland functional connectivity by reducing the potential for plant species to disperse through stepping stones within the landscape and via livestock vectors (Römermann et al. 2008; Auffret and Cousins 2013; Plue and Cousins 2018).

Within a fragmented landscape, small natural features can form part of a network of “green infrastructure” and positively contribute to landscape connectivity. Although green infrastructure is a broad term, it is widely used in environmental policy (e.g. the European Union Strategy on Green Infrastructure https://ec.europa.eu/environment/nature/ecosystems/strategy/index_en.htm). It can be defined as a network of core habitat and other features that might support biodiversity and ecosystem services at the landscape scale (Garmendia et al. 2016; Bullock et al. 2018). As such, the definition of these green infrastructure habitats relevant to semi-natural grassland connectivity includes restored grasslands, forest borders, midfield islets (small, often rocky areas with a thin topsoil layer within crop fields), managed hedgerows and road verges. Although these landscape features do not have all the environmental attributes of ancient semi-natural grassland, they may support at least some populations of semi-natural grassland species (Cousins 2006; Auffret and Cousins 2013; Jakobsson et al. 2016; Hunter et al. 2017; Poschlod and Braun-Reichert 2017; Lindgren et al. 2018; Thiele et al. 2018). Hence, green infrastructure habitats may enhance both structural and functional connectivity by increasing available habitat and linking otherwise isolated grasslands through supporting dispersal processes or the movement of dispersal vectors through the landscape (Auffret and Cousins 2013; Hunter et al. 2017; Poschlod and Braun-Reichert 2017; Bullock et al. 2018; Damschen et al. 2019). Given the loss of species-rich grassland across much of Europe, such green infrastructure may therefore provide important additional functional connectivity (Bullock et al. 2018). However, the contribution of this green infrastructure to landscape connectivity, particularly for specialist grassland species that may be more restricted to core semi-natural grassland areas and heavily dependent on dispersal vectors such as livestock, remains unclear (Plue et al. 2019). Likewise, while road verges, hedgerows and forest borders might be structurally connecting elements, their role in providing both structural and functional connectivity will depend on species' dispersal abilities and ability to establish in these habitat types (van Dijk et al. 2014).

Understanding how land use change has affected structural and functional connectivity and the impacts on grassland plant communities is key to understanding how contemporary rural landscapes can be managed to conserve biodiversity (Lindborg and Eriksson 2004; Cousins et al. 2015). Here, using landscapes in three European countries, we assess changes in land use composition that have occurred over the last 50 years in terms of both semi-natural grassland loss and changes in green infrastructure. We then quantify how resulting changes in landscape composition have affected landscape connectivity, using resistance surfaces that estimate both structural and functional connectivity. We expect to see a decline in grassland area across all regions, accompanied by an associated decline in landscape connectivity, and particularly in functional connectivity. Finally, we investigate the ability of structural and inferred functional connectivity to explain variation in grassland plant communities, in terms of grassland specialist species and more generalist species, in both restored and ancient grasslands. Grassland patches are expected to have higher total (gamma) diversity where they are embedded in high connectivity landscapes, due to the greater numbers of species able to reach sites via spatial dispersal (Baur 2014: Auffret et al. 2018). Greater habitat availability and connectivity within the landscape also enables species to develop larger populations and to occupy a greater proportion of available microsites (Erikson, 1996). Higher levels of connectivity are therefore also expected to increase smaller-scale species richness within patches (alpha diversity), and reduce turnover of species (beta diversity) between different parts of grasslands. This may, however, depend on an interaction between connectivity and grassland age, because more recently restored grasslands may not have had enough time to develop the high density of species typical of ancient grassland habitats (Schmid et al. 2017; Damschen et al. 2019). Grassland specialists, which are likely to be less able to utilise structural connecting elements, should be more dependent on functional connectivity and on the age of grassland sites (Evju et al. 2015). Conversely, generalist species which may benefit from landscape linear and remnant features may be more closely related to landscape structural connectivity, and be less influenced by the history of grasslands.

Methods

Study regions

The grassland landscapes were situated in three European countries, Belgium (Viroin region), Germany (Regensburg county, Kallmünz region) and Sweden (Södermanland county and the Stockholm archipelago). In each of these three regions, we selected 12 focal semi-natural grassland patches, six ancient (continuously managed through grazing for centuries) and six restored (abandoned at some point in the past but with grazing management recently re-established) (Adriaens et al. 2006; Poschlod et al. 2008). These were chosen to cover landscapes with a range of grassland and other semi-natural habitats, and therefore represent a gradient of present-day connectivity for grassland plants. Size of the focal grasslands ranged from 0.28 ha to 5.85 ha. All focal grasslands were subject to grazing management, by sheep or cattle. Restored grasslands were mostly restored by removal of successional scrub and tree growth on abandoned pasture, but some sites (mostly in Germany) were restored onto former arable fields.

Connectivity data

Our approach to assessing connectivity and its role in these landscapes involved determining metrics representing both structural and inferred functional connectivity, determining how these have changed in each landscape, and assessing the ability of each metric to explain variation in species composition in the focal grasslands. We digitised land cover within a 1600 m buffer drawn from the centroid of each focal grassland. Grassland species composition has been shown to be related to landscape composition over similar distances in the past (e.g. Adriaens et al. 2006). Digitisation was performed for past time periods using black and white aerial photographs (from 1965 in Belgium, 1952–1963 in Germany and 1952 in Sweden) and present time periods using colour aerial orthophotographs (from 2015 in Belgium and 2017 in Germany and Sweden). Past dates represented the earliest time period for which consistent historical landscape information could be obtained for all three regions. Land classes identified in historical aerial photographs were arable land, water, built-up land, open grassland, semi-open grazed forest (hereafter open forest), midfield islets (small, often dry or rocky areas contained in arable fields (Cousins 2006)), wetland and dense, closed forest. We identified the same classes for present day landscapes, with the dense forest class split into deciduous, coniferous and logged forest (this was not possible for earlier black and white photographs). No semi-open grazed forest remained in contemporary landscapes, so this category was not present in the contemporary landscape digitization. We also digitised road verges, hedges, railway banks and complex forest borders (forest borders where the transition from open to forest habitat is gradual, resulting in heterogeneous conditions with some more open areas (Lindgren et al. 2018)), for both time points.

We considered semi-natural grassland, open forest, midfield islets, forest borders and road verges as potential "green infrastructure" (GI) habitats for grassland plant species, in relation to our focal habitats (Cousins 2006; Poschlod and Braun-Reichert 2017; Lindgren et al. 2018). We created two metrics of connectivity following Hanski (1994), which we adapted to represent structural and inferred functional connectivity. Both of these metrics were calculated within each individual landscape.

$$Connectivity = \sum_{x=1}^{n}\left(\left(e^{-d_x}\right) \times gridsize\right) \qquad (1)$$

with x a gridcell containing GI at distance; n the number of gridcells containing GI; d from the target site (in km); and *grid size* 0.000625 ha (2.5 × 2.5 m), which, although constant, is retained to allow potential comparability with other studies. Landscapes consist of circles with a 1600-m radius from the centre of the target site.

To model connectivity, we assumed the green infrastructure was potential grassland habitat. The contribution of each GI element to connectivity was calculated and summed across all grid cells (n) containing GI (x) of each landscape using Eq. 1. Two versions were calculated: (1) structural connectivity, which used Euclidian distances to all GI habitats from the edge of focal grassland (d) and (2) inferred functional connectivity, whereby distance (d) was represented by the length of the least cost path between the edge of the focal grassland and a grid cell containing GI (x). We further refer to this least cost path as cost distance. For each grid cell containing GI, cost distance was calculated using the ArcGIS 10.6.1 spatial analyst Costs distance procedure (see Supplementary Material S1). Input into this procedure is a habitat-specific resistance layer from which the cost distance between the focal site and grid cell containing GI is computed. This resistance layer represents the reduced probability of dispersal of grassland plant seeds across higher resistance habitats by livestock as dispersal vectors, and follows the methodology in Adriaensen et al. (2003) and Sawyer et al. (2011).

For most road verges and semi-natural grasslands, there was no resistance to plant dispersal and establishment. For other landscape elements, the resistance was increased by 5-times for semi-permeable habitats (e.g. forest borders, hedgerows), larger for nearlyimpassable habitats/land uses (forest, arable, urban: 100 times) and 1000-times for impregnable habitats/land uses (water, wetlands and railroads). We explain the full cost resistance procedure and all the resistance values employed in Supplementary Material S1. This was done for all 36 landscapes individually for both time periods, providing metrics of the levels of structural and functional connectivity in each landscape, for both the past and present-day.

We assessed changes in land use over time by classifying digitised land use in rasters of 5 metre spatial resolution and summing transitions or stasis from past to present for several key habitat types. This provided an indication of the contemporary status of areas that were dense forest (combined deciduous and coniferous), open forest, arable land, improved grassland or semi-natural grassland habitats in the past (Fig. 1). We also calculated total changes in the areas of major land use categories and green infrastructure habitats separately for each country (Fig. 2a), along with change in landscape structural and functional connectivity (Fig. 2b).

Plant species data

We recorded all vascular plant species present within ten 1 m^2 quadrats, randomly located within each focal grassland patch (total 360 plots). This ensured that biodiversity sampling was independent of grassland patch size. We standardized species names across countries using the R package Taxonstand (Cayuela et al. 2019), and the International Plant Names Index nomenclature (IPNI 2020). We calculated total species richness for each focal grassland by summing the number of unique species found across all ten sampling plots, as a measure of the overall (gamma) diversity present within the grassland, and average smaller-scale species richness (alpha diversity) as the mean number of species found per plot. An additional full grassland survey was also carried out to identify all species present in the grassland. This added an average of 22.4 species per grassland on top of the plot totals. However, this full survey was not used in subsequent modelling, to avoid the risk of reducing comparability across countries due to different grassland sizes and greater potential observer bias. Results from this survey were used to confirm that plot totals

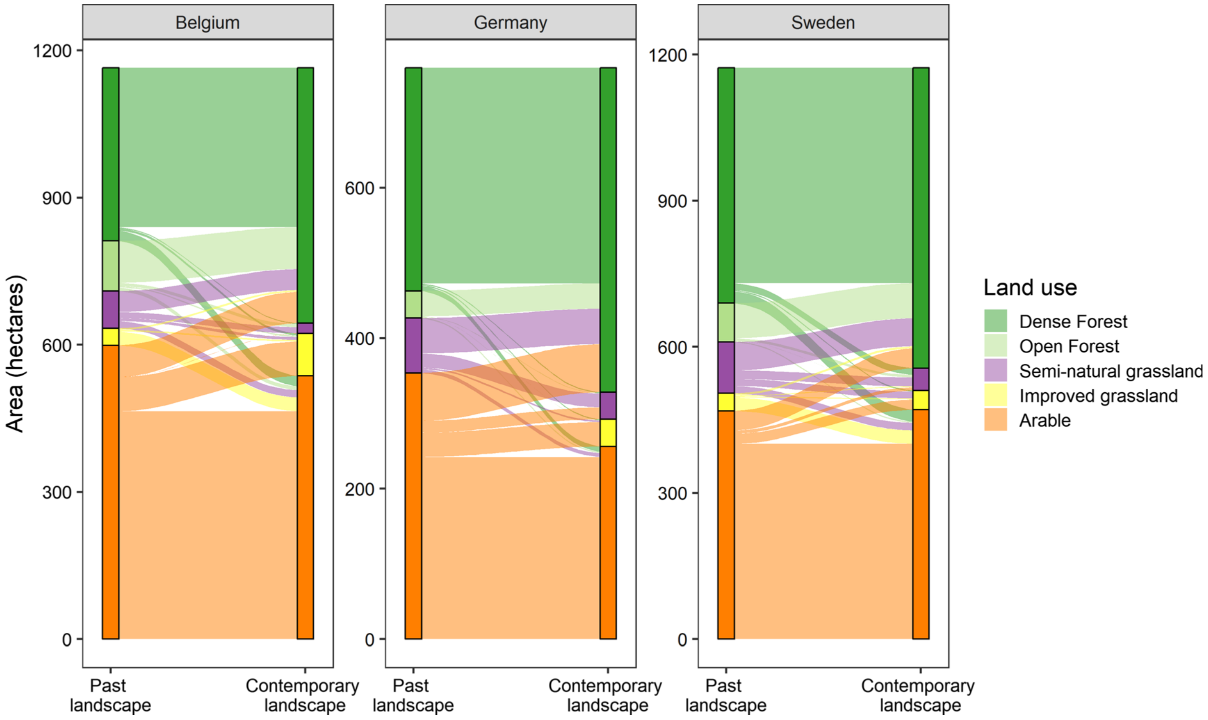

Fig. 1 Change in key habitats in the study landscapes from past (Belgium = 1965, Germany = 1952–1963, Sweden = 1952) to contemporary (Belgium = 2015, Germany and Sweden = 2017) periods

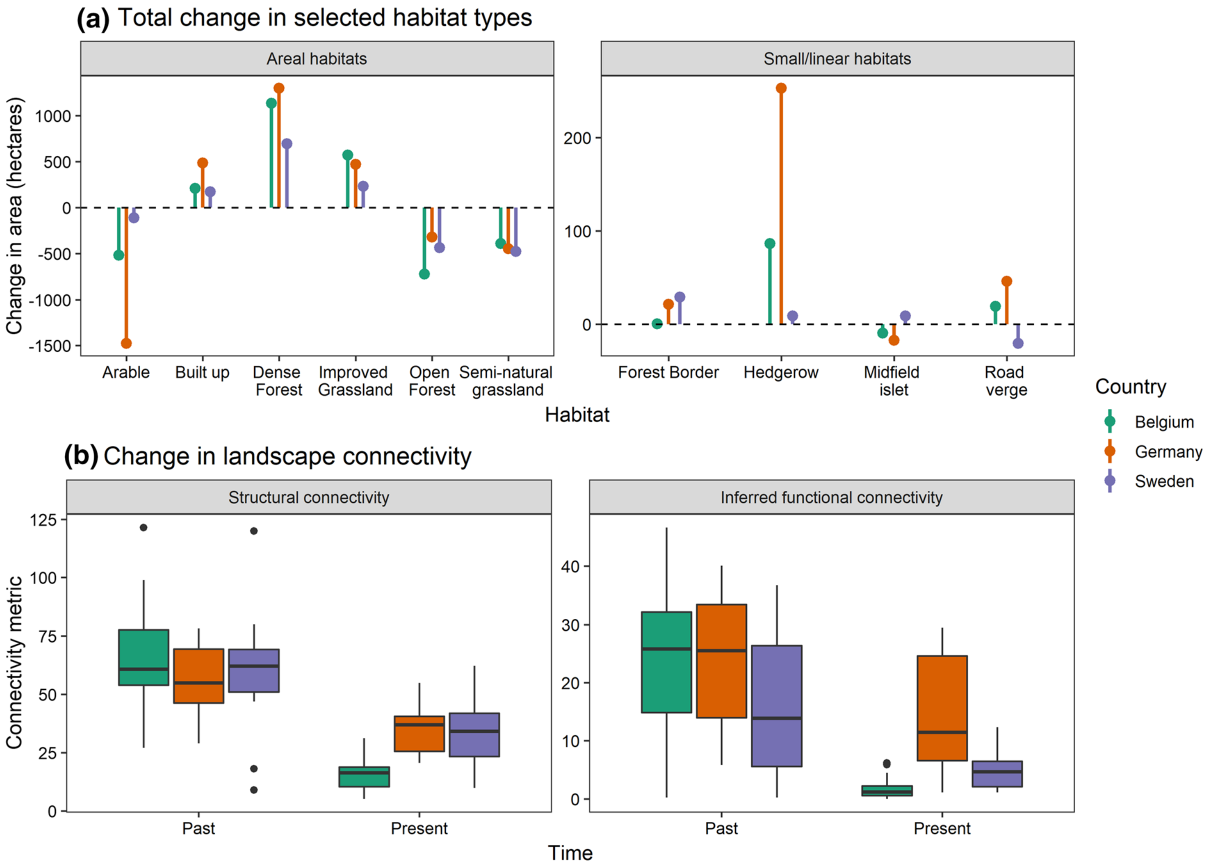

Fig. 2 **a** Change in habitat amount in 36 landscapes (12 in each Belgium, Germany and Sweden), and **b** associated changes in both structural and functional connectivity

across the ten plots were sufficient to represent grassland gamma diversity (Pearson correlation between plot total and full survey = 0.77, $p < 0.001$). We also calculated beta-diversity between plots in each focal grassland as the overall Sørensen dissimilarity between the ten survey plots using the *beta.multi* function in the R package betapart (Baselga et al. 2018). This allowed grasslands with species rich but patchy composition to be distinguished from grasslands with a highly diverse species composition across all plots. Gamma, alpha and beta diversity were also calculated for two subgroups of species (grassland specialist and generalist species) based on habitat preferences extracted from the TRY database (Kattge et al. 2011, 2020), trait ID 3096, containing two primary sources (Hill et al. 2004; Klimešová and Bello 2009). Grassland species were those favouring acid, calcareous, dry or neutral grassland broad habitat types, but not those capable of utilising arable or built-up habitats (Hill et al. 2004), nor those considered ruderal by Klimešová & de Bello (2009). Generalist species were those capable of utilising arable or built-up land uses (potentially in addition to other habitat types) along with those considered ruderal (Klimešová and Bello 2009). Although this is a coarse measure of habitat preference, taking a broad approach avoids problems with combining different expert classifications across multiple countries. For the 6.5% percent of occurrences with no data in TRY (including species only resolved to genus level), species were not assigned to either grassland specialist or generalist species (but are included in the overall category). See Supplementary Material S2 for a full list of species categories and a summary of their occurrence across countries. We used gamma, alpha and beta diversity for these three groups (overall, grassland and generalist species) as response variables in subsequent statistical analyses.

Statistical analyses

Statistical analysis consisted of two steps. First, since structural and functional connectivity are non-independent measures and cannot be included together in statistical models, we analysed their effects separately to determine which of these two variables had the most explanatory power for each biodiversity metric. In order to do this, we fitted two linear models for each response variable (9 response variables in total; alpha, beta and gamma diversity for all species, grassland specialists and generalist species) using landscape structural connectivity and functional connectivity, respectively, as single predictors. Comparing within these model pairs, the connectivity variable that produced the highest R-squared value for each response variable (Supplementary Material S3, Tables S3-1, S3-2 & S3-3) was then carried forward to a full model. This full model also included grassland patch area as a continuous predictor and history (restored or ancient) as a two-level factor, with ancient grasslands as the reference factor level. The potential importance of study country as a random effect was investigated by comparing a generalised least squares model without a random effect to a linear mixed effects (lme) model with country as a random intercept in a likelihood ratio test (Zuur et al. 2009). Only the models for patch total beta-diversity and grassland specialist beta-diversity were improved with the addition of country as a random effect. As a result, total beta-diversity and grassland specialist beta-diversity models were fit using the lme function in the R package nlme (Pinheiro et al. 2018), while all other models were fit as linear models using the lm function in R. Patch area and both structural and functional landscape connectivity were square root transformed to reduce the skew in their distribution. All variables in all models were centred and standardised by dividing by two standard deviations using the rescale function in R (Gelman 2008), to enable better comparison and selection between variables on different scales, and allow interpretation of coefficients in the presence of an interaction term (Schielzeth 2010). The interaction between landscape connectivity and patch history was also included, to account for any differences in the response of ancient and restored grasslands to varying connectivity. This resulted in nine final models of connectivity effects on gamma (Table 1), alpha (Table 2), and beta diversity (Table 3) in focal grassland patches. Model residuals were visually checked, confirming normality and homogeneity of distribution.

Results

Analysis of landscape change over the last 50 years demonstrated a consistent loss of semi-natural grassland across all three areas. This was driven mainly by the conversion of grasslands to forest, with a smaller proportion of grassland becoming arable land or improved grassland (Fig. 1). This figure also highlights the fact that many grasslands, particularly in Germany, have developed from former arable fields or from formerly forested land, with few grasslands with a long continuity of management remaining in the landscapes. There was also a complete loss of grazed semi-open forest habitat (which was not mapped in contemporary landscapes due to its absence) (Fig. 2a). Statistics from the resistance surfaces show that land use changes have had a large effect on landscape connectivity, with losses in both structural (mean decrease of 48.7%) and inferred functional connectivity (mean decrease of 33.4%) (Fig. 2b). Furthermore, almost all present-day landscapes have a lower connectivity than even the least well-connected landscapes in the past. This is despite the fact that linear green-infrastructure habitats became more frequent, particularly road verges and hedgerows, with the largest increases in these habitats occurring in the German landscapes (Fig. 2a).

Structural rather than functional connectivity was a more effective predictor of total gamma diversity within focal grasslands (Table 1). There was no significant relationship between connectivity and grassland specialist gamma diversity, but higher generalist gamma diversity was found where grassland structural connectivity was lower. Furthermore, the negative relationship between generalist species gamma diversity and structural connectivity was stronger in ancient patches than in restored, suggesting that a long continuity of grassland management in a highly connected landscape has an additional suppressive effect on the number of generalist species present. Although grassland specialist gamma

Table 1 Results of models of plant species diversity (total richness across 10 vegetation plots within grasslands from 36 landscapes) for different species groups

Variable	Estimate	t	p	R^2
Total species gamma diversity				0.294
Structural connectivity	− 0.516	− 3.183	**0.003**	
Management history (restored)	− 0.072	− 0.478	0.636	
Patch area	0.072	0.439	0.664	
Structural connectivity × history	0.500	1.569	0.127	
Grassland specialist gamma diversity				0.186
Structural connectivity	− 0.189	− 1.086	0.286	
Management history (restored)	− 0.314	− 1.938	0.062	
Patch area	0.128	0.730	0.471	
Structural connectivity × history	0.475	1.389	0.175	
Generalist species gamma diversity				0.503
Structural connectivity	− 0.625	− 4.591	**< 0.001**	
Management history (restored)	**0.322**	**2.539**	**0.016**	
Patch area	**− 0.332**	− 2.420	**0.022**	
Structural connectivity × history	**0.712**	**2.664**	**0.012**	

Bold text indicates a significant result at the 95% confidence level. Management history shows the difference between ancient and restored grasslands, with ancient grasslands as the reference factor level

Table 2 Results of models of plant species density (mean richness per vegetation plot within grasslands from 36 landscapes) for different species groups

Variable	Estimate	t	p	R^2
Total species alpha diversity				0.078
Inferred functional connectivity	0.185	0.892	0.379	
Management history (restored)	− 0.249	− 1.357	0.185	
Patch area	− 0.015	− 0.067	0.947	
Inferred functional connectivity × history	− 0.122	− 0.314	0.756	
Grassland specialist alpha diversity				0.424
Inferred functional connectivity	**0.476**	**2.912**	**0.007**	
Management history (restored)	− 0.574	− 3.964	**< 0.001**	
Patch area	0.001	0.006	0.996	
Inferred functional connectivity × history	− 0.177	− 0.578	0.568	
Generalist species alpha diversity				0.089
Inferred functional connectivity	− 0.092	-0.446	0.659	
Management history (restored)	0.275	1.512	0.141	
Patch area	− 0.210	− 0.972	0.339	
Inferred functional connectivity × history	0.046	0.121	0.905	

Bold text indicates a significant result at the 95% confidence level. Management history shows the difference between ancient and restored grasslands, with ancient grasslands as the reference factor level

diversity tended to be higher in ancient than restored grasslands, this relationship was not significant at the 95% confidence level. Lower generalist gamma diversity was seen with increasing grassland size, and in ancient patches compared to restored (Table 1).

Of the alpha diversity variables, only grassland specialist species were significantly affected by landscape connectivity (Table 2). Grassland specialist alpha diversity was most strongly affected by inferred functional connectivity, rather than structural connectivity. Management history was also important for grassland specialist alpha diversity, with ancient patches containing a higher alpha diversity of grassland specialist species per than restored grasslands. Beta diversity of all species between plots within the same grassland was lower in high structural

Table 3 Results of beta diversity (Sørenson dissimilarity between vegetation plots within grasslands) modelling

Variable	Estimate	t	p	R^2
All species beta-diversity[a]				0.150
Structural connectivity	**− 0.358**	**− 2.305**	**0.029**	
Management history (restored)	0.169	1.444	0.159	
Patch area	0.040	0.233	0.817	
Structural connectivity × history	0.477	1.904	0.067	
Grassland specialist beta-diversity[a]				0.231
Inferred functional connectivity	**− 0.435**	**− 2.953**	**0.006**	
Management history (restored)	**0.411**	**3.714**	**0.001**	
Patch area	− 0.065	− 0.409	0.685	
Inferred functional connectivity × history	0.281	1.177	0.249	
Generalist species beta-diversity				0.094
Structural connectivity	− 0.325	− 1.772	0.086	
Management history (restored)	− 0.001	− 0.004	0.996	
Patch area	− 0.101	− 0.543	0.591	
Structural connectivity × history	0.155	0.430	0.670	

Bold text indicates a significant result at the 95% confidence level. Management history shows the difference between ancient and restored grasslands, with ancient grasslands as the reference factor level

[a] Indicates model fit using nlme with Country as a random effect

connectivity landscapes, while beta-diversity of grassland specialists was lowest in high functional connectivity landscapes, and in restored patches (Table 3).

Discussion

Landscapes have undergone extensive losses of semi-natural grassland habitat over the last 50 years in our study areas across the three European countries, leading to substantial declines in both structural and functional connectivity for grassland plants. We show that observed increases in green-infrastructure habitats suitable for grassland plant species, such as hedgerows and road verges, are far from sufficient to compensate for the widespread abandonment of semi-natural grassland (Adriaens et al. 2006; Hooftman and Bullock 2012; Cousins et al. 2015). Although these habitats may contribute to functional connectivity (Vanneste et al. 2020), particularly at the local scale or in landscapes with very little remaining grassland, our results do not support the increasing focus on the potential of a well-connected network of green infrastructure to mitigate losses in core habitats at the landscape scale (Garmendia et al. 2016; Bullock et al. 2018). Consequently, landscapes today are less likely to facilitate grassland species dispersal, with no landscapes comparable in inferred functional connectivity to any but the least connected areas in the past. High connectivity is paramount to allow species to survive in fragmented landscapes, maintain vital plant/pollinator interactions and genetic diversity, and adapt or shift ranges in response to changes in climate and environmental conditions (Ozinga et al. 2009; Saura et al. 2014; Rotchés-Ribalta et al. 2018). The connectivity losses we observed, therefore, likely represent a serious decline in the ability of grassland plants to adapt to key current and future global change drivers.

Ancient grasslands are vital sources of biodiversity, since grassland specialist communities take many years to become fully established following the reintroduction of grazing management in restored sites (Aavik et al. 2008; Waldén et al. 2017; Karlík and Poschlod 2019). This was reflected here in differences observed between ancient and restored grasslands. Although total species richness was not affected by grassland age, ancient patches contained fewer generalist species, a higher alpha diversity of grassland species and a lower beta diversity between plots within each grassland compared to restored sites. This supports previous work suggesting that gamma diversity within grasslands increases relatively quickly following the re-introduction of traditional management measures, but that specialist species are slow to establish as larger populations (Austrheim and Olsson

1999; Pykälä et al. 2005; Aavik et al. 2008; Schmid et al. 2017). Importantly, our results indicate that this is not only determined by temporal processes and management continuity, but is also dependent on landscape connectivity. Mean grassland specialist alpha diversity was lower in patches embedded in poorly connected landscapes, even in older grasslands. This may be because in landscapes that have suffered from connectivity declines, many species may exist only in relatively small numbers as "sink" populations. Such species are likely to be at greater risk of future local extinction due to the disruption of important meta-population dynamics and the reduced likelihood of additional migration from combined neighbouring populations (Eriksson 1996; Evju et al. 2015). This creates multiple conservation problems. Firstly, connectivity declines are a direct threat to biodiversity in ancient grasslands, contributing to species extinctions (Plue and Cousins 2018). Secondly, connectivity declines reduce the capacity for grassland restoration. Ancient grasslands in low-connectivity landscapes are likely to be less able to act as an effective source of colonising individuals, effectively decreasing the size of the landscape species pool. The lower ability of these species to disperse across the landscape then further reduces the likelihood of species reaching target patches, representing a serious obstacle to efforts to restore landscape biodiversity (Baur 2014; Waldén et al. 2017). More active methods of restoration such as species translocation or the spreading of cut hay or hayseed from species rich grasslands, a common agricultural practice in historical times but now less frequently applied outside of conservation management (Poschlod and Bonn 1998), may represent a way of overcoming these functional connectivity declines. These methods are likely to assist the initial colonisation of restored sites by grassland specialist species. However, the extent to which these methods would be able to provide long-term benefits to high landscape functional connectivity and to an established historic grazing network, is unclear.

Grassland species alpha diversity responded more strongly to the functional connectivity metric than to structural connectivity. This suggests that physical connecting elements such as hedgerows and open forest borders are not providing significant additional functional connectivity for grassland species in these landscapes. This may partly be due to quality of these habitats for grassland plants relative to core semi-natural grassland patches, which was built into the functional connectivity metric but not included in the structural connectivity metric (Auffret and Cousins 2013). While marginal habitats can support a range of grassland species, this can depend on the presence of favourable local environmental conditions (Jakobsson et al. 2018; Lindgren et al. 2018). If this is the case, managing these habitats more effectively for grassland species may help to increase functional connectivity, particularly in landscapes which have very little grassland remaining. However, the stronger relationship of grassland species density with the functional connectivity metric may also represent the importance of moving livestock as dispersal vectors for these plants (Fischer et al. 1996; Römermann et al. 2008; Plue et al. 2019). Taking this into a wider landscape context, well-connected core semi-natural habitat, maintained by moving livestock, is an important priority to preserve.

The occurrence of generalist species in semi-natural grasslands was negatively affected by structural connectivity. This also appears to underpin a negative relationship between structural connectivity and overall species diversity. There are several possible explanations for this. Firstly, the higher dispersal capability of generalist species means that they are less affected by landscape configuration, allowing them to reach all suitable patches regardless of landscape configuration (Römermann et al. 2008; Saura and Rubio 2010). Furthermore, establishment is a key element of effective dispersal (Auffret et al. 2017). Hence, it may be that generalist species are able to utilise green infrastructure connecting elements but are unable to fully establish in core-semi-natural sites due to their grazing intolerance (Vandewalle et al. 2014). Since only focal grasslands were sampled in this study, generalist species may be more common in the wider landscape in highly connected landscapes. However, where these species are less able to survive in ancient grasslands, i.e. sites with a long-history of regular, low intensity local management and grassland species present at higher densities, the higher landscape connectivity provided by green infrastructure is likely to have no direct impact on the number of species present in focal grasslands. In fact, as appears to be the case here, the positive effect of connectivity on grassland species may lead to a reduction in the number of generalist species present due to competition with the greater density of grassland species (that are more able to tolerate low-intensity grazing and dry, infertile conditions). Finally, the connectivity metrics were derived with grassland species in mind, and as such may be less appropriate for generalist species. Including other landscape elements as potential habitat may have further clarified these patterns.

Although linear landscape elements can act as pathways for undesirable plants to spread (Lelong et al. 2007; Maheu-Giroux and de Blois 2007; Joly et al. 2011), the presence of such habitats within the landscape does not appear to lead to an increase in the occurrence of generalist species in grasslands in these study areas. Differences between patterns observed for different species groups also highlight the fact that important biodiversity responses to landscape functional connectivity may underlie patterns in overall species richness. The functional connectivity metric here primarily considered dispersal via moving livestock, since this is a primary mechanism of biodiversity maintenance in species rich grassland habitats (Plue and Cousins 2018), and because the introduction of rotational grazing is often a focus of habitat restoration and landscape management plans. However, dispersal via bird, wildlife and humans through agricultural and conservation management provide some degree of additional spatial dispersal potential for many species (e.g. Auffret and Cousins 2013), and may depend upon different spatial assumptions than those applied here regarding landscape resistance. Hence, while the functional connectivity metric used here was able to explain patterns in grassland specialist diversity, different spatial assumptions may result in connectivity estimates which vary in their ability to explain patterns across species groups, and species with different dispersal specialisations.

The landscape changes we identified likely represent only the most recent part of an ongoing loss of grassland habitat. The total reductions in grassland connectivity are likely to be far more extensive (Adriaens et al. 2006; Poschlod et al. 2008; Cousins et al. 2015). Given this long-term history of habitat loss in these study landscapes, it is possible that time-lags remain in the response of some grassland species to past habitat fragmentation (Lindborg and Eriksson 2004; Helm et al. 2006; Piqueray et al. 2011). Any remaining extinction debts still to be settled in areas which have lost habitat may mean that the full negative effects of connectivity loss have not yet become fully apparent, although this likely only applies to older grassland habitats (Helm et al. 2006; Cousins 2009). Potential time lags and small-scale variation in environmental conditions within grasslands (particularly restored sites) may well represent important additional predictors of species diversity which were not accounted for in models here (Gazol et al. 2012). Despite this, grassland species alpha and beta diversity was well explained by the combination of landscape connectivity and patch history. This shows the key importance of these variables for grassland biodiversity, highlighting the role landscape connectivity plays in both maintaining healthy older grasslands (Hooftman et al. 2015; Plue and Cousins 2018) and allowing grassland species to colonise recently created habitat (Pywell et al. 2002; Waldén et al. 2017). Protecting remaining functional connections, particularly between older grasslands, seems the key to maintain grassland biodiversity. Passive restoration efforts on former grassland sites are likely to meet with limited success unless restored sites are connected functionally to ancient grasslands either via adjacent habitat or the movement of grazing livestock.

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