Policy analysis

Dispersal limitation, eutrophication and propagule pressure constrain the conservation value of Grassland Green Infrastructure

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ABSTRACT

Semi-natural grasslands harbour many of Europe's species of conservation interest. Although larger grasslands are the focus of most conservation activity, many grassland fragments are scattered across landscapes –in small patches or along linear elements– which can form *Grassland Green Infrastructure* (GGI). GGI has the potential to enhance landscape diversity by creating functioning metacommunities comprising of large semi-natural grasslands and these surrounding fragments. While often highlighted in conservation policy, little is known about the biodiversity supported by green infrastructure itself and thus its conservation potential.

To address this issue, we contrasted plant communities in 36 'core' grassland sites across three European countries with communities in the surrounding GGI. We related compositional differences to amount and type of GGI habitat (patches or linear), and the distances for seed dispersal by livestock from core sites. We found substantial differences between the GGI and the core sites, with a mean 54% species turn-over. These differences indicated filtering of stress tolerant species characteristic of low nutrient conditions, and semi-natural grassland specialists. Species with poorer dispersal abilities declined strongly with increasing distances from the core sites. The many additional species in the GGI, not found in the core sites, were predominantly those with a competitive strategy and high seed dispersal ability.

We conclude that the biodiversity-supporting role of GGI across Europe is severely constrained by eutrophication, dispersal limitation and external propagule pressure. Actions to improve the quality of GGI might include enhancing dispersal by livestock combined with more type-diversification and less intensively used grassland habitats.

1. Introduction

Habitat loss and fragmentation due to land use intensification is a major driver of plant biodiversity declines worldwide (Newbold et al., 2015; Auffret et al., 2018; Chase et al., 2020). In Europe, semi-natural grasslands are hotspots for plants, insects and other organisms (Wilson et al., 2012), and harbour a large proportion of plant species of conservation interest (Habel et al., 2013). In addition to their role in supporting biodiversity, semi-natural grasslands provide many environmental, cultural and recreational benefits (Bengtsson et al., 2019). Despite this, semi-natural grasslands have become fragmented and have declined substantially due to drivers including agricultural intensification and afforestation (Poschlod and WallisDeVries, 2002; Cousins et al., 2015; Ridding et al., 2020a).

Unsurprisingly, biodiversity conservation generally focusses on the large areas of remaining grassland, but this is not the only semi-natural grassland vegetation present in human-modified landscapes. Smaller grassland fragments, comprising road verges, old-field hedges and complex forest borders are often scattered throughout the landscape, many being remnants of previously larger grassland areas (Cousins, 2006; Auffret and Lindgren, 2020). These smaller fragments –though potentially lower in habitat quality– have the potential to form a network of Green Infrastructure (GI) around large semi-natural grasslands, and facilitate functioning species' meta-communities that harbour more diversity at the landscape scale (Lindborg et al., 2014; Fahrig, 2017). Green Infrastructure – 'networks of natural and semi-natural areas with other environmental features'– is a key concept in European Union policy, for example, designed to enhance biodiversity and ecosystem services (European Commission, 2013). While there is much research on designing and mapping GI across landscapes (Snäll et al., 2016; Hermoso et al., 2020), it is rare to consider the quality of these landscape elements in relation to their ability to function as GI. As a result, it is unclear whether simply mapping putative GI elements gives sufficient information on the ability of the elements to form a functional GI network. Concepción et al. (2020) for instance showed how surveys of landscape elements could be used to determine their value as GI for different species groups. Here, we consider the status of Grassland vegetation Green Infrastructure (GGI) over a range of European landscapes and the drivers that affect that status. Grassland vegetation is here defined in the broadest sense containing all habitat that could harbour (remnants of) populations of grassland species of conservation interest.

From a grassland conservation perspective, the value of GGI elements can be considered in terms of their plant compositional similarity to the larger semi-natural grasslands in the landscape (Vanneste et al., 2020). Although they might have different species compositions, GGI elements may still contain self-sustaining populations of specialist semi-natural grassland plants, or they may be sinks with local plant populations rescued by periodic seed flow from nearby larger grasslands (Hooftman et al., 2003; Plue and Cousins, 2018). In the latter case, GGI that is more distant from the large grasslands will either lack these species or have small populations that are less resilient to changes in the local environment and the incoming propagule pressure and competition from other, more generalist species. In combination with increased demographic stochasticity in small populations, this results in an increased likelihood for populations to go locally extinct (Leimu et al., 2006; Auffret et al., 2017). Two important forces will interact in degrading this rescue process: poorer connectivity which leads to a lower dispersal ability (Ozinga et al., 2009; Auffret et al., 2017) and environmental deterioration towards a less favourable habitat which lessens the effectiveness of this dispersal (Römermann et al., 2008; Poniatowski et al., 2018). These dispersal filtering processes ultimately determine which species will be present in a location (Bullock and Pufal, 2020). The dispersal ability of a species, which constrains its likelihood of reaching more distant GGI elements from the larger grasslands, is generally vector-dependent (Tamme et al., 2014). Vectors include abiotic vectors such as wind and water, but around grasslands, dispersal may be assisted by grazing livestock (cattle, sheep or goats) transporting seeds into GGI habitats as they are herded among larger grasslands (Willerding and Poschlod, 2002; Rico et al., 2012; Plue et al., 2019). Livestock are known to be relatively non-discriminating as vectors (Plue et al., 2019), dispersing in dung and on hair/wool both specialised zoochorous species as well as seeds not clearly adapted for zoochory (Albert et al., 2015).

Even if dispersal happens, its effectiveness in maintaining specialist species' populations in the GGI is constrained by local biotic and abiotic filters. Intensive agriculture in the landscape matrix can elevate nutrient inputs (Newton et al., 2012; Ridding et al., 2020b). Other negative environmental and management drivers include increased shading due to edge effects, infrequent grazing or cutting, or severe disturbances (Jakobsson et al., 2018; Lindgren et al., 2018). Such environmental filters may favour species not typically found in semi-natural grasslands

(Vanneste et al., 2020).

Where landscape connectivity and habitat quality are sufficient for both seed dispersal and plant establishment and persistence, the only differences in species composition between the GGI and the large grasslands should be in species number due to passive sampling (Chase et al., 2020). In GGI elements with low connectivity and/or a different, degraded environment, however, species capable of longer distance dispersal or with more generalist characteristics may be favoured. The ability of species to persist in low connectivity landscapes and/or with reduced habitat quality can therefore be expected to be related to their functional characteristics (Saar et al., 2012; Hooftman et al., 2016). Functional traits can help to understand the response of plants to their environment, such as in terms of disturbance regime and nutrient supply. For example, perenniality, clonal growth and survival in the seed bank may affect the ability of plant populations to persist at a given location (Johansson et al., 2011; Piqueray et al., 2015). However, every species possesses a unique combination of traits, each of which affects its response to environmental drivers, meaning that analysing a few, single traits may be misleading (Wright et al., 2006). Therefore, more holistic approaches utilising composite traits have been developed, of which Grime's Universal Adaptive Strategy theory is one of the best-known (Grime, 1977; Pierce et al., 2017). Habitat association can also be regarded as a holistic metric indicating a composite of response traits, following *e.g.*, Hill et al. (2004). Similarly, Tamme et al. (2014) combined a variety of plant and seed traits to predict dispersal ability, based on maximum dispersal distances.

In this study we contrast the plant species compositions of large semi-natural grasslands ('*core sites*') with samples of their surrounding GGI in 36 landscapes among three countries across North-Western Europe. To determine the drivers of differences between the GGI and semi-natural grasslands, we explore the differences in species and composite trait composition in relation to the amount and type of habitat present in the GGI, combined with inferred livestock seed dispersal distances (*sensu* Adriaensen et al., 2003). We investigate the following questions:

1) Do GGI elements have lower α-diversity and different species composition compared to core sites?
2) How do GGI communities differ from core sites in terms of plant adaptive strategies, habitat preferences, and dispersal abilities?
3) How do distance from the core site and amount and type of habitat available correlate with community composition?
4) What are the main constraints on conservation value of the GGI, as suggested by 2) and 3)?

2. Materials & methods

2.1. Research area and grassland green infrastructure classes

2.1.1. Landscapes

Our work draws upon species surveys and digitisations of 36 landscapes in Western Europe (Kimberley et al., 2021): the Viroin valley in Belgium, referred to hereon as the *Western-region*; the Kallmünz region in Germany (*Southern-region*) and Södermanland county and the Stockholm archipelago in Sweden (*Northern-region*). Twelve landscapes were located in each of three regions, all harbouring a similar calcareous low fertility grassland of conservation interest on neutral to alkaline (Northern region) or alkaline soils (Western and Southern), incorporating environmental and cultural variation. In Fig. 1 we provide examples of the landscapes and the geographical locations of the regions.

Each landscape centred on a large semi-natural grassland site, subject to grazing management by livestock: sheep, goats or cattle. The landscape was defined within a 1500-meter radius buffer around the large grassland centroid, which we digitised to map the land uses contained therein (described in Kimberley et al., 2021; Fig. 1). The size of the these central grasslands was on average 1.5-hectares (±1.3 (SE)), with the smallest sites in the Southern region (0.6-hectares ± 0.3 (SE));
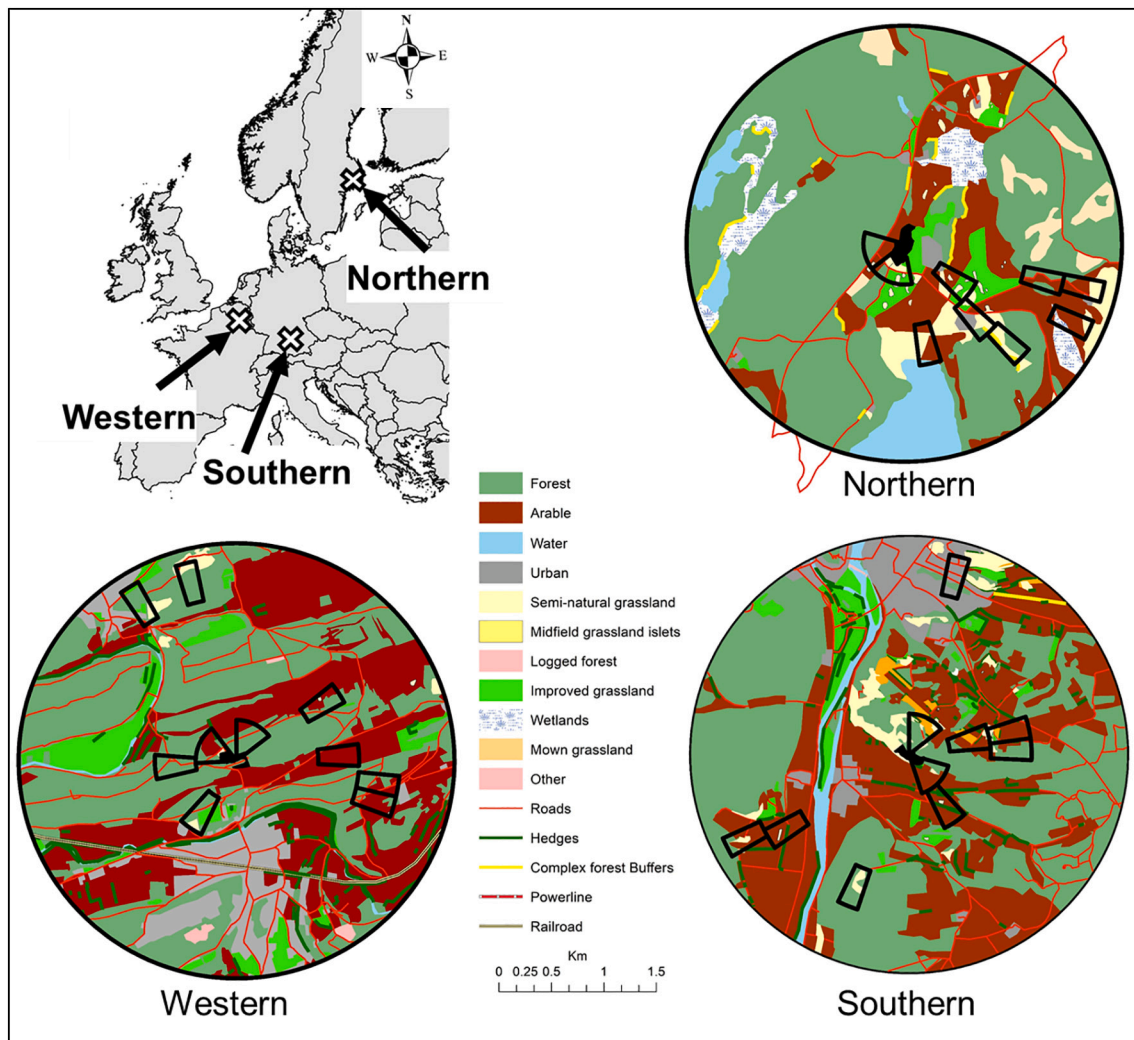
Fig. 1. Location of the research regions in Western Europe (a) with (b-d) example landscapes from each of the regions with core site (black) and selected GGI segments of 4-hectares, two in each of five concentric rings of 300-m. Roads were connected outside the landscape where appropriate for shortest route estimation.

Northern: 1.9-hectares ± 1.1; Western: 2.1-hectares ± 1.7). We refer to these as the '*core sites*'. For the Western- and Southern region the selected core sites encompassed most of sites of conservation interest in the selected region. In the buffer, various amounts of grassland vegetation were nested within a predominantly arable or forested matrix (Fig. 1). Grassland vegetation is defined in the broadest sense as all vegetation with the potential to contain populations of grassland species of conservation interest. We established ten 4-hectares sample areas at different distances around each core site in these buffers, 351 segments in total. In these segments we conducted species surveys (described in 2.2.1 below; SI-1) in all the structural elements defined as GGI (described in 2.1.2; Fig. 1). The sample areas are depicted in example landscapes in Fig. 1.

2.1.2. Structural classes

From the digitised maps of the landscapes (all are depicted in SI-2) we selected the Grassland Green Infrastructure (GGI) elements – *i.e.*, those landscape elements expected to contain some form of grassland vegetation – using three classes with sums per segment:

1) Linear road verges (mostly being along dirt roads, assuming a 2.5-meter verge width);

2) Other linear features: hedges, complex forest borders, railroad verges and powerline cuttings in forest (15-meter, 10-meter, 2.5-meter and 20-meter width, respectively);

3) Smaller non-core site grassland patches ('patch GGI', in m^2), including midfield islets (Cousins, 2006).

For statistical analysis (2.3) we combined all three classes into a Total GGI value per segment. The assumed widths above were used to translate linear length to square meters with widths checked in the field (SI-1). In general the Southern region contained highest coverage for all GGI categories (Table SI-1-1). The proportion of forest and arable in the matrix did not differ among regions (Table SI-1-1).

2.1.3. Livestock dispersal distance

To estimate dispersal limitation, we generated cost resistance distances using assumed landscape resistance values following Adriaensen et al. (2003). Assumed resistances among different landscape elements were vector oriented, theoretical and amplifying difference spanning four orders of magnitude (1−1000). See *e.g.* Poniatowski et al. (2016) for a functional complexity approach. We explain the full cost resistance procedure in SI-3. A table with the resistance values employed is provided as Table SI-3-1. As livestock is the main vector of focus in this study, our set of assumptions is tailored to herding and grazing of cattle,

sheep and goats. While dispersal by livestock may be rare in some cases, the potential dispersal distances are much higher than by, for example, wind (Tamme et al., 2014; Bullock et al., 2017). Other dispersal processes, for example by human machinery, may have a role in some landscapes (Bullock et al., 2003). But to avoid over-parameterisation of our connectivity metric, we focus only on livestock-mediated dispersal. Poor performance of this livestock metric might indicate the importance of other dispersal processes. Here, we assumed livestock movement was not restricted on dirt- or minor roads, while being herded between larger grasslands, or in core site grassland habitats where they graze. In other land use types, movement was assumed to be severely restricted (Table SI-3-1). The distance metric we used as a predictor variable for the composite trait analyses (2.3) was the mean cost resistance distance to a GGI structural element. Together with the three structural classes (2.1.2) this '*livestock dispersal distance*' encompasses our connectivity variable. To achieve normal errors distance is $\log_{10}$-transformed throughout this study.

2.2. Species surveys and community traits

2.2.1. Segments and surveys

In July and August 2017, we surveyed plant species composition in the core sites. Methodological details can be found in SI-1 and Kimberley et al. (2021). We conducted species surveys in the GGI elements in the landscape buffers in July and August 2018. Therefore, both surveys encompass those species visibly present in mid-summer.

Because buffers could not be surveyed in their entirety, we selected sample areas which we refer to as '*segments*'. Aiming to sample at a range of distances from the core site, we generated five concentric 300-meter bands up from the edge of the core site (Fig. 1; SI-1). Each band was divided into segments of 4.04-hectares. In each band, we randomly selected two segments for vegetation surveys with an added requirement for the minimum amount of GGI; Fig. 1 contains examples of the actual selections used. For this added requirement, we used surveying time as unit, calculated with a standardised surveying speed of 20-minutes per hectare within the smaller grasslands, and of 1-minute per 7.5 m along linear features. Based on our digitisations, potential segments that did not contain at least 10-minutes of total surveying time were excluded. In total we surveyed ≈5% of the entire 804-hectares of each landscape. In total 351 selected segments were surveyed for plant species present in each GGI element. The other nine segments – of the selected 360– were not accessible. A detailed description of the segment selection, surveying methods, alignment of nomenclature and a full species list is provided in as Table SI-1-2.

2.2.2. Community traits and triangulation

Our selected species community traits were all derived from TRY (Kattge et al., 2020): in Table SI-4-1 we report their full database reference and number of encountered taxa with data available. In all cases, our calculations are based on species presence. We also used the following indicator and composite traits:

1) Ellenberg environmental indicators for Nutrients, Moisture, Light and Soil reaction (pH) (Ellenberg et al., 2001);
2) Maximum seed dispersal distance using the R-package *dispeRsal* developed by Tamme et al. (2014);
3) Indicators of habitat association following Hill et al. (2004) and Klimešová and De Bello (2009);
4) Grime adaptive strategy (Pierce et al., 2017).

For (1) and (2), community trait values were estimated as the mean across species. To depict compositional shifts for (3) and (4), we employed triangulation whereby species composition is represented as the mean position among species present along three axes, summing to 1. For adaptive strategy, the seven categories in TRY (TraitID-196) were translated to the CSR-axis following Pierce et al. (2017). The translation factors are provided in Table SI-4-2. Similarly, habitat preference in 18 categories following the Broad Habitat Types set by Hill et al. (2004) were translated into 3 categories (Table SI-4-2): Grassland species; Woodland & Boundary species; Ruderal & Arable species. We used this Broad Habitat Type terminology throughout, which means, *e.g.*, that woodland and forest are synonymous. The proportion of species per category was used as location coordinates along three axes (Table SI-4-2). As a result, each segment had a single location within the adaptive strategy and habitat preference triangles.

2.3. Statistical analysis

All calculations were performed in Matlab 7.14.0.739, codes have been made available *via* GitHub (https://github.com/dhooftman72). To identify filtering processes causing differences in species composition between the core sites and the GGI, community trait values were calculated for two groups (1) the '*core-site species*' which comprised *all* the species found in the 36 core sites (426 species), and (2) '*outside-species*', found *only* in the GGI, so not in any core site (299 species; Table SI-4-2). Note that many core-site species were also found in the GGI (Table SI-1-2). Prior to calculations, all community trait values in segments for these species groups were normalised against the community trait value of their respective core site as $\left[\frac{segment\ value}{core\ site\ value}\right]$, making community trait values in segments relative to that core site.

Per community trait, the compositional similarity between each segment and core site was statistically tested as binominal contrast (core *vs* segment) using the *anovan* tool with type I Sum of Squares in which the normalised compositional trait value (Y with $n = 387$: 351 segments & 36 cores)) explained by this contrast after filtering for variation explained by *Region* (as fixed variable) and all non-quantified *Landscape* effects nested in *Region* as random variable, representing all the unquantified differences between landscapes. An interaction term tests for similarity among the three regions in effect strength and direction. The results of this analyses correspond to Table 1. This can be described as regression equation:

$$[Y \sim \beta_c + \text{Region} + \text{Landscape(Region)} + \beta_1(\text{contrast}) + (\text{Region} \times \text{contrast})]$$

Subsequently, using the same general structure as above, we related GGI structure to community mean traits of the core-site species group found in the GGI per segment (Y, with $n = 351$ segments), in a two tiered procedure in which:

Tier 1. model with region, landscape nested in region, distance (in meters) and *Total GGI* per segment (in square meters) is analysed as:

$$[Y \sim \beta c + \text{Region} + \text{Landscape(Region)} + \beta_1(\text{Distance}) + \beta_2(\text{Total GGI})$$

$$+ (\text{Region} \times \text{Distance}) + (\text{Region} \times \text{Total GGI}) + \varepsilon];$$

Tier 2. The three GGI structure classes, nested within Total GGI, are analysed based on the residuals (ε) of the first tier as:

$$[\varepsilon \sim \beta_3(\text{Road Verge}) + \beta_4(\text{Other Linear GGI}) + \beta_5(\text{Patch GGI}) + (\text{Region} \times \text{Road Verge}) + (\text{Region} \times \text{Other Linear GGI}) + (\text{Region} \times \text{Patch GGI}) + \varepsilon']$$

The results of this analyses are given in Table 2. This combination of Type 1 Sum of Squares (among tiers) and Type 3 Sum of Squares (within tiers) answers the question whether any of the three GGI class variables deviates from the general trend of *Total GGI* and shows any additive effects. The relationships depicted in figures are as a GGI class variable against marginal values (Y-ε). Residuals (ε') were normally distributed according to a Jarque-Bera test for all traits. The number of species (α-diversity) was log$_{10}$-transformed prior to normalisation. The general threshold for significance is $P < 0.05$, unless otherwise noted. In SI-5 we present an sensitivity analyses in which landscapes were split in two groups based on respective core site size.

3. Results

3.1. Large species turn-over between core sites and GGI

Of the 725 species recorded, 426 occurred in at least one of the 36 core semi-natural grassland sites, but only 39 of these were unique to these sites and not found in any of the GGI segments. On average 76.3 (sd: ±10.5) species occurred in a core site (Fig. 2a), ranging from 63.1 (±8.1) species in the Southern-, 75.3 (±13.5) in the Northern-, to 90.4 (±10.0) in the Western region. By contrast, 299 species were recorded exclusively in the GGI. Therefore, core-site species also occurred in the GGI, but conversely, that there was a large pool of species found in the GGI that was not present in any of the core sites (outside-species).

Each GGI segment had on average 17% lower α-diversity (sd: ±13%) than its respective core site (Fig. 2a; F-value: 10.8, $P < 0.001$); this ranged from no α-diversity difference in the Northern region to 41% lower diversity in the Southern region. In contrast, when considering only core-site species, the difference between the core sites and their individually surrounding GGI was much greater: 61% (±7%) of core-site species were absent from the GGI (F-value: 537, $P < 0.001$), ranging from 54% in the Northern-, 60% in the Western-, to 70% in the Southern region. Over half of the species present in the GGI (54% ±9.8%) were not present in the respective core site (F-value: 345, $P < 0.001$; Fig. 2a).

The Southern region had the lowest proportion of outside-species in the GGI (48%) compared to both other regions (54% for the Northern- and 57% for the Western region).

3.2. Low similarity of community traits between core sites and GGI

The GGI contained species with, on average, greater dispersal abilities than those in the respective core sites. Core sites contained species with a mean 74 m maximum dispersal distance, while the value was 110 m for core-site species also found in the GGI, and 129 m for outside-species, with no among region interaction (Table 1). Changes in this composite dispersal trait were driven mostly by changes in species' seed mass (Table 1; SI-6). The mean seed mass of outside-species was almost 4-times higher than of the species in the respective core site (+273%), but with a large variance (±286%). In addition, core-site species that were also found in the GGI had a higher mean seed mass than those found in the respective core sites (+49% ±45%).

Composite trait values suggested habitat conditions differed strongly between the core sites and the surrounding GGI. Ellenberg indicator values of the species in the GGI indicated shifts towards a much more nutrient-rich, moister and slightly more shaded environments. This difference was partly driven through filtering of core-site species, but mainly by outside-species with a different set of environmental requirements (Table 1). In particular, outside-species had a mean 37% higher nutrient and 17% higher moisture indicator values than species in the core sites. The role of outside-species in driving the high nutrient signal (nutrient-indicator) was especially strong in the Northern region (+44%) compared to both other regions (+33% Western and + 34% for the Southern region). Differences in Ellenberg light and pH indicator values were much smaller and similar between core-site and outside-species (Table 1).

Similarly, mean habitat preferences and adaptive strategy values were substantially different in the GGI than in their respective core sites, with little variation in this effect among regions (Table 1). This difference was again partly due to filtering of core-site species, but was more strongly related to composite trait differences of the outside-species. For habitat preferences, in the GGI there was a shift from typical grassland species towards species typical of ruderal and arable habitats, as well as

Table 1

The α-diversity, habitat indicator and community trait changes as mean percentage change (sd, averaged over regions) among core sites and GGI segments for core-site species and outside-species, *i.e.,* species not found in any core site. F-statistics are for the linear contrasts [core sites *vs.* GGI segments] with df contrast/error = 1/342 (2.3; SI-8). §: strongly significant among-region interactions ($P < 0.01$). Full F-statistics for all factors are provided in SI-8.

	Core site value	Core-site species		Outside-species	
		Difference from core site	F-value	Difference from core site	F-value
Nr of Species (α-diversity)	76.2 (10.5)	−61% (6.9%)[§]	538***	+45% (9.8%)[§]	345***
Ellenberg indicators					
Nutrients	3.81 (0.25)	+11% (6.0%)	24.8***	+37% (14%)[§]	207***
pH	5.03 (0.17)	−4.4% (3.8%)	11.4***	−0.2% (6.1%)[§]	0.03
Light	6.84 (0.11)	−2.7% (1.9%)	14.8***	−4.1% (4.0%)	15.6***
Moisture	3.78 (0.11)	+1.3% (1.9%)[§]	4.26*	+17% (5.5%)	150***
Habitat preference[a]					
Grassland	0.53 (0.03)	−11% (6.2%)	24.7***	−34% (9.3%)	188***
Woodland & Boundary	0.26 (0.03)	+9.4% (14%)	3.59	+54% (22%)	106***
Ruderal & Arable	0.21 (0.02)	+15% (14%)	8.93**	+25% (21%)	23.9***
Grime Adaptive Strategy[a]					
C-species	0.53 (0.02)	+13% (6.6%)	44.6***	+10% (9.3%)	26.9***
S-species	0.26 (0.02)	−11% (6.7%)	19.6***	−22% (12%)	60.5***
R-species	0.21 (0.02)	−19% (9.8%)	39.1***	+5.1% (15%)	1.69
Max. dispersal distance (m)[b]	73.9 (10.3)	+48% (28%)	18.1***	+74% (44%)	28.7***
Seed dry mass (mg)[c]	21.4 (8.5)	+49% (45%)	6.21*	+273% (286%)[§]	14.3***

[a] Sum to unity.

[b] Following Tamme et al., 2014, back-transformed from log$_{10}$.

[c] Main driving variable for dispersal distance, for other included traits see SI-6; ($P < 0.01$).

* $P < 0.05$.

** P < 0.01.

*** $P < 0.001$.

Table 2

F-statistics (with sign indicating direction) for α-diversity, habitat indicators and community composite trait changes for core-site species against structural elements of the GGI segments, using a two-tiered model to test for additive effects of structural elements nested in total GGI with SS type I among tiers and Type III within tiers (2.3). §: strongly significant among-region interactions (P < 0.01). Full F-statistics for all factors are provided in SI-8.

| | Livestock dispersal distance (m) | Total GGI (m²) | Nested in total GGI | | |
			Road Verges (m)	Other Linear features (m)	Patch GGI (m²)
Number of species (α-diversity)	6.84**(−)	42.4***(+)§	22.0***(+)	0.17	6.06*(+)
Ellenberg indicators					
Nutrients	8.89**(+)	25.3***(−)§	0.79	13.0***(+)	2.28
pH	5.11*(−)§	9.77**(+)	3.83	0.04	2.28
Light	3.11	4.85*(+)	6.15*(+)	1.89	2.26
Moisture	3.03	3.87	2.51	5.88*(+)	3.76
Habitat preference					
Grassland	6.21*(−)§	11.4***(+)§	1.08	3.07	4.72*(+)
Woodland & Boundary	1.76	0.43	8.48**(−)	0.26	3.13
Ruderal & Arable	0.01	16.7***(−)§	5.29*(+)	7.37**(−)	0.44
Universal adaptive strategy					
C-species	1.66	34.2***(−)§	4.07*(−)	5.76*(+)	5.02*(−)
S-species	2.02	13.9***(+)	6.68*(+)	13.2**(−)	2.29
R-species	0.66	25.4***(+)§	0.83	0.16	3.34
Max. dispersal distance (m)[a]	12.4**(+)	1.84	7.27**(−)	5.86*(+)	4.90*(−)
Seed dry mass (mg)[b]	3.96*(+)	2.73	10.8**(−)	0.15	0.55

[a] Following Tamme et al., 2014.
[b] Main driving variable for dispersal distance, for other included traits see SI-6.
* P < 0.05.
** P < 0.01.
*** P < 0.001.

to species typical of woodland and boundary habitats (Table 1; Fig. 3a). Similarly, there was a shift in the adaptive strategy from stress tolerators (S-species) towards competitor species (C-species; Table 1; Fig. 3b). Ruderal species (R-species) showed no clear patterns.

3.3. The structure of the GGI governs the degree of filtering of core-site species

The degree to which core-site species were represented in the surrounding GGI was related to the inferred livestock dispersal distance from the respective core site. A higher estimated distance resulted in a larger decline in α-diversity (Table 2, Fig. 2b). The area of GGI per segment was positively correlated to α-diversity of core-site species (Table 2, Fig. 2c); more area per segment meant fewer species were lost. These relationships were significantly less pronounced in the Northern region (Fig. 2). Within the total GGI area, the relative amount of road verges and patch GGI both had a positive, additive effect on α-diversity of core-site species, suggesting that diverse GGI structural classes further enhances core-site species presence.

The mean maximum dispersal distance per segment was positively correlated with the livestock dispersal distance to the core sites, with no difference in this relationship among the three regions (Table 2, Fig. 4a). A correlation of this dispersal trait with total area of GGI was less apparent (Table 2) although a weak relationship might be detected (Fig. 4b). This may be because the different GGI classes had different relationships with the dispersal trait; road verge and patch GGI had a negative relationship with the mean dispersal trait, whereas other linear features had the opposite effect.

Concerning Ellenberg habitat quality indicators, GGI grassland communities that were further from the core sites, according the livestock dispersal distance, were characterised by species of more eutrophic and acidic conditions than GGI closer to the core sites (Table 2; Fig. 4c & e). By contrast, where more GGI habitat was present in a segment, the communities were characteristic of more oligotrophic, alkaline and less shaded conditions (Table 2; Fig. 4d & 4f), *i.e.*, the conditions were more similar to those of core sites. The Northern region was an exception, with no relation between habitat indicators and the

amount of GGI with a segment (Fig. 4c & e). Within the total present GGI habitat per segment, the relative amount of linear features was positively related to eutrophication and moisture, whereas having more road verges was linked to indicators of a less shaded environment (Table 2).

Different groups of species had different correlations to both livestock dispersal distance and the GGI structural classes. Species that prefer grassland habitats and are stress-tolerators, both indicative of typical semi-natural grassland species, showed decreases similar to that of the overall α-diversity (Table 2; Fig. 3). Ruderals and competitors showed the opposite patterns (Table 2, Fig. 3). But in all cases, these relationships held true for two of the three regions, with the Northern region exhibiting no effects. As well core site size affected the strength of the distance correlations (SI-5). Higher relative cover of road verges and lowering of the other linear features exacerbated the effect of total GGI area in decreasing the distance-decay of stress tolerators and lessening the increase of competitive species (Table 2).

4. Discussion

While conserving and establishing green infrastructure is promoted as a key approach for species conservation at the landscape scale (*e.g.*, Concepción et al., 2020), we found that plant communities in Grassland Green Infrastructure (GGI) were notably different to those in the core semi-natural grasslands. This suggests that the GGI by itself in grassland landscapes across NW-Europe is currently of only moderate value for conservation or as habitat for semi-natural grassland species. Green infrastructure is not simply 'green space'; it must comprise areas in the landscape which focal species can live in and/or move through to reach suitable habitat patches. This is true for animals, whereby the habitat quality of infrastructure such as corridors affect movement behaviour (Poniatowski et al., 2018; Habel et al., 2020). For plants, which have limited movement ability, the ability to colonise and live in the infrastructure is important. Our analyses suggest the dispersal and environmental filters constrain the composition of the GGI compared to the core grassland sites. Hence, the differences between the GGI and core site communities were only in part due to straightforward effects of the lesser available area, as would be expected under a no-filter scenario
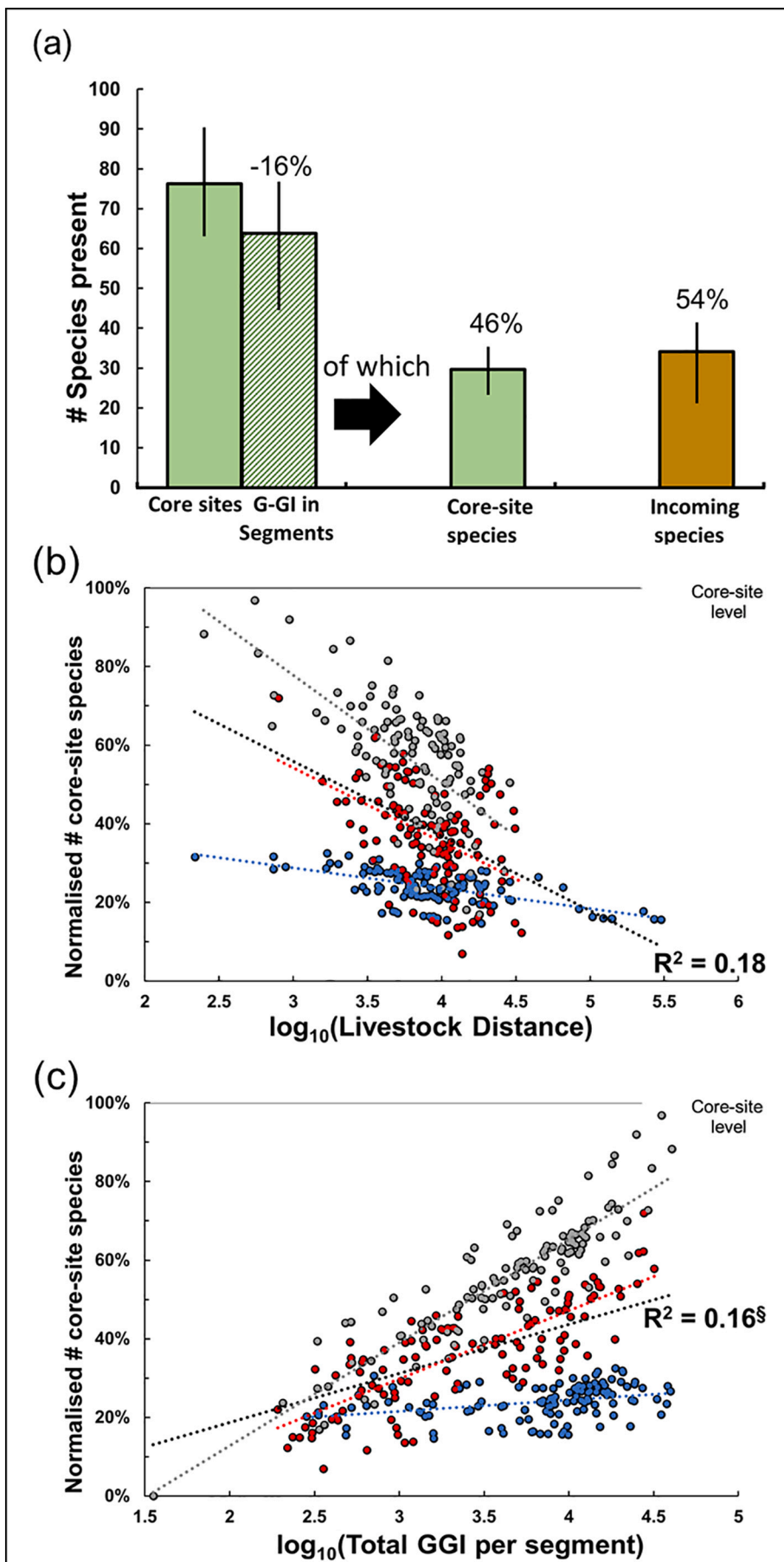
Fig. 2. α-diversity and its correlations with structural connectivity classes. a) α-diversity of core sites and GGI segments, split into core-site species and outside-species, error bars indicate the among-region ranges (highest-lowest); b) normalised core-site species α-diversity in segments correlated to livestock dispersal distance (100% = core site values); c) normalised core-site species α-diversity in segments correlated to total GGI area per segment. The black line indicates the relationship for all sites with its accompanying R² for the overall relationship; the **Blue** line and points represent the Northern region, **Red** the Western, and **Grey** the Southern region. § indicates a significant interaction between effect size and regions.
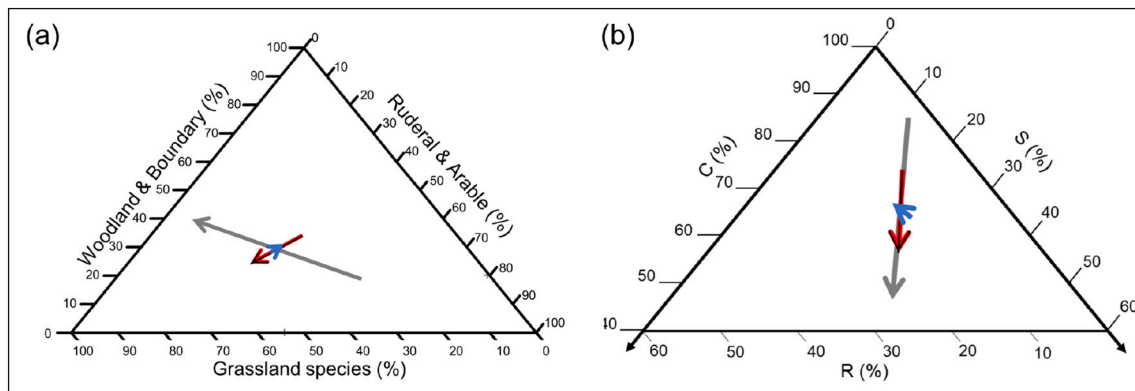
Fig. 3. Triangular depiction of direction and strength of normalised mean species composite trait: a) species habitat preference with arrows indicating the direction and arrow length indicating the strength of the correlation per region as <main effect + interaction> with total GGI area per segment; b) ditto for the Universal Adaptive Strategy. For significance see Table 2; data points are included in Fig. SI-9. **Blue** arrow represent the Northern region, **Red** (with black hearted arrow) the Western, and **Grey** the Southern region. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Chase et al., 2020). Our results show that the extent of species filtering in these smaller habitats is correlated to the levels of connectivity with the core sites, and to species' life-histories, with these two factors interacting. Therefore, low connectivity, and reduced potential for both dispersal and establishment, appears to be limiting the ability of grassland species to utilise elements of existing GGI.

4.1. Vegetation under pressure by eutrophication and dispersal limitation

The vegetation composition of the GGI indicated a more nutrient-rich habitat than the core sites. Similarly, these GGI habitats appeared to be moister and more shaded compared to their respective core sites, probably due to a taller and more vigorously-growing vegetation. These findings suggest a fundamental environmental filter, by which more nutrient rich conditions, and possibly lack of appropriate management in these degraded habitats, benefit species which can thrive in GGI grasslands habitats at the expense of more specialist species of semi-natural grassland. Habitat degradation through eutrophication and inappropriate management is a common problem for grassland conservation in Europe (Newton et al., 2012; Ridding et al., 2020b), and our findings for the GGI mirror these issues. This contrasts somewhat with Vanneste et al. (2020), who found road verges contained similar numbers of grassland specialists as in adjacent grasslands, although they also found more generalists in the verges. This maybe because their verges were contiguous to the core sites and thus they were possibly more similar environmentally and also less affected by dispersal limitation (their furthest verge plot was only 50 m from the core sites).

Our analyses also suggest, along with to degraded habitat quality, dispersal processes further constrain development of high conservation-value vegetation in the GGI. The stress-tolerators (Pierce et al., 2017) and semi-natural grassland specialists (Hill et al., 2004) are subject to strong dispersal filters, as represented by the inferred livestock dispersal distances from the core sites. Generally, these are also the species of conservation interest (Habel et al., 2013). Additionally the strength of the distance filters depends on the size of the core site as seed source; smaller core sites are a poorer seed source (SI-5). By contrast, their more ruderal or nutrient-loving counterparts (competitive and ruderal species) are less affected by dispersal filters, next to having less establishment limitation. The filtering is reinforced by the reduced ability of species with poorer dispersal abilities (*i.e.,* a lower maximum seed dispersal distance, *sensu* Tamme et al., 2014) to occupy GGI at further livestock dispersal distances from the core site. These findings all indicate dispersal limitation of poorer-dispersing species is important in shaping the composition of the GGI. Dispersal limitation is less acknowledged as a filter in vegetation dynamics than environmental filters, but can have strong effects on species composition (Helsen et al.,

2013; Bullock and Pufal, 2020). These correlations were apparent in two of our regions, but were weak in the Swedish region possibly because environmental filtering was stronger here or past connectivity was lower (Kimberley et al., 2021).

Moreover, the species pool from the predominantly agricultural or forested landscape matrix likely allowed a propagule influx for species more suited to the environment of the GGI, leading to increased competitive pressure on the semi-natural grassland species. This apparent propagule pressure with more suited species resulted in a > 50% turn-over of species between the GGI and the respective core sites. These species found only in the GGI differed greatly in their trait values from those core site species that persisted in the GGI, being characterised by fast-growing, competitive species with good dispersal capacities.

4.2. Enhancing dispersal networks

Small GGI habitat area, suboptimal habitat quality, and isolation all seemed to contribute to limiting the ability of grassland plant species to make use of the GGI in the wider landscape. Our results suggest that the overall loss of large, species-rich grasslands across the study areas (Kimberley et al., 2021), and abandonment of grazing networks across Europe –whereby livestock is moved among grasslands (Willerding and Poschlod, 2002; Plue et al., 2019)– constrain the ability of grassland plant species to utilise GGI, in addition to straightforward effects of habitat quality.

It is interesting that dispersal limitation was a strong filter in these landscapes. Livestock –cattle, sheep and goats – disperse seeds of a wide variety of species (Auffret et al., 2012; Rico et al., 2012) and were a dominant yet currently decreasing feature of European semi-natural grasslands (Karlík and Poschlod, 2019; Plue et al., 2019). Livestock are certainly not the only dispersal vector in our study areas, with humans and their machinery, other animals and wind also being possible vectors. However, large vertebrates, including livestock, disperse seeds further on average than many other vectors (Bullock *et al* 2017), and additional analyses using landscape resistance assumptions for these other vectors showed less correlation to the observed species diversity and trait patterns (SI-7). While we certainly do not claim livestock management would the only solution to increasing the value of GGI, livestock management and directed 'rewiring' (*sensu* Bullock et al., 2018) of the GGI could enhance connectivity and thus the conservation value of the GGI. In practice, this might involve introducing and optimising grazing networks and herding routes (Römermann et al., 2008; Plue and Cousins, 2018). Furthermore, connectivity could be enhanced by also managing existing GGI areas to enhance the habitat quality (*e.g.,* for road verges; Jakobsson et al., 2018). Our results also indicate it would be beneficial to create a diversity of GGI types, as more road
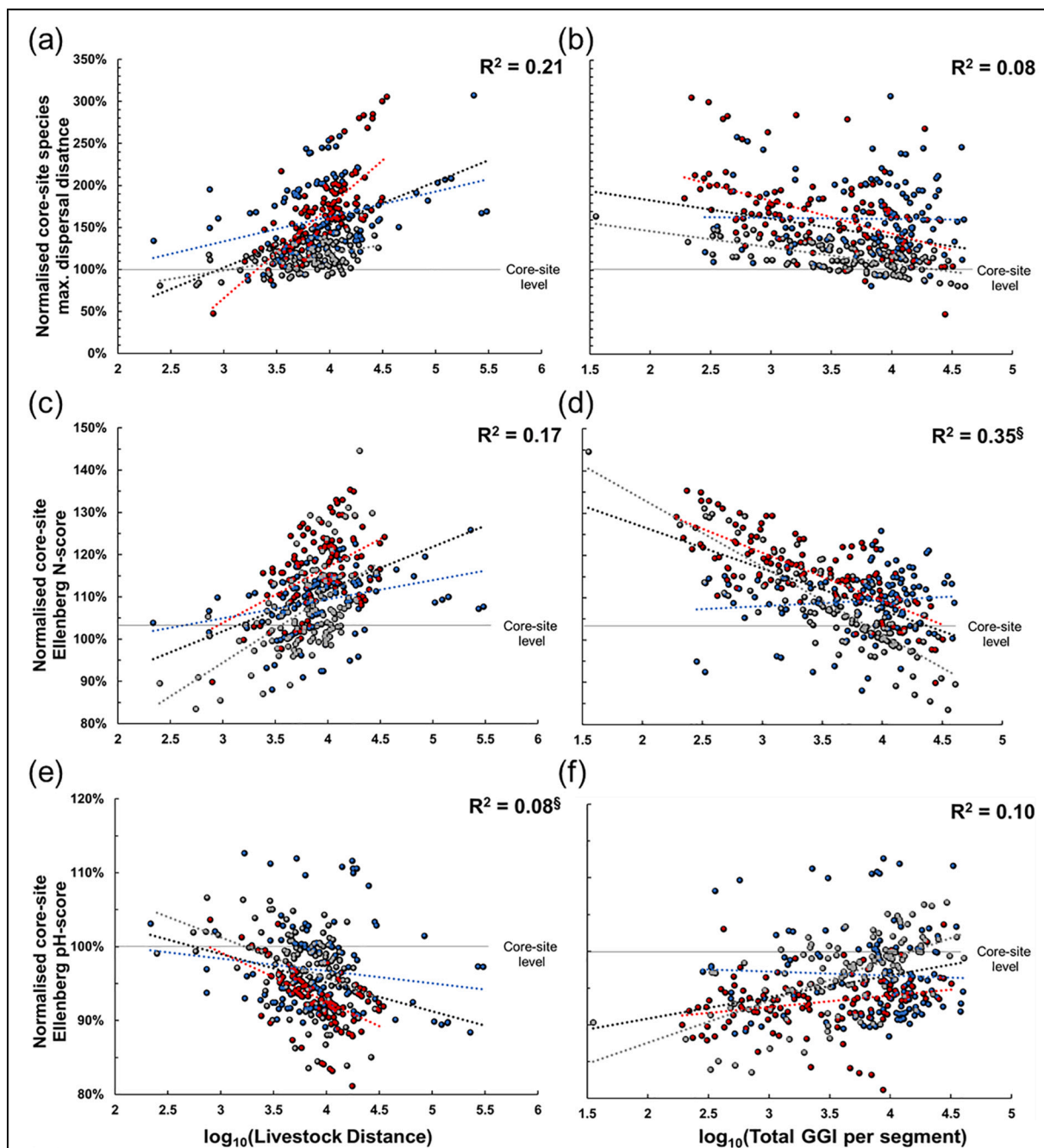
Fig. 4. Selected normalised community mean trait values correlated against livestock dispersal distance and total GGI area per segment for: a/b) maximum dispersal distance following Tamme et al. (2014), c/d) Ellenberg nutrient indicator, e/f) Ellenberg pH indicator. The **Black** line indicates relation for all sites with its accompanying R^2 of the overall relationship; **Blue** line and points represent the Northern region, **Red** the Western, and **Grey** the Southern region. § indicates a significant interaction between effect size and regions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

verges combined with patch habitats promote species with traits associated with semi-natural grasslands. Although other linear features, such as hedges, seem to be less suitable for grassland species, they might have a positive effect on species of other habitats (Vanneste et al., 2020) or other species groups (Löffler et al., 2020).

Part of the GGI in our study areas comprised remnants of a formerly less fragmented patches (Kimberley et al., 2021). Many GGI features (both grassland remnants and small, often rocky, mid-field islets) have been present for several centuries (Adriaens et al., 2006; Cousins et al., 2015), including roads (Auffret and Lindgren, 2020). For remnant grassland fragments in the GGI, the correlations we identified could

reflect the process of slow on-going erosion of diversity from previously better-connected habitat often referred to as an 'extinction debt' (Auffret et al., 2018; Kimberley et al., 2019; Löffler et al., 2020). The conservation strategies we have discussed – livestock networks, more and a more diverse GI, as well as reducing nutrient influx from the matrix – may help prevent the payment of extinction debts in these remnants.

5. Conclusions

Habitat fragmentation and loss of connectivity are major threats to habitats of conservation value (Haddad et al., 2015; Fletcher et al.,

2018; Chase et al., 2020). Green infrastructure provides a possible solution, but we found that Grassland Green Infrastructure in three European countries had limited value as indicated by species compositions and trait profiles. Our analyses demonstrated that the habitat quality differences, dispersal limitation and propagule pressure from nongrassland communities constrained similarity of the GGI elements to the large grassland sites. These findings were quite consistent across the three European regions. This raises the question whether Green Infrastructure can benefit biodiversity (see Concepción et al. (2020) for a similar conclusion). Our findings indicate how conservation management might improve the status of the GGI: landscape grassland diversity might be improved by considering livestock dispersal networks as well as by creating more and more diverse grassland habitats.

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CRediT authorship contribution statement

Danny Hooftman: Conceptualization, Methodology, Software, Formal analysis, Data curation, Visualization, Writing – original draft. **Adam Kimberley:** Methodology, Project administration, Data curation, Writing – review & editing. **Sara Cousins:** Conceptualization, Funding acquisition, Supervision, Writing – review & editing. **Gema Escribano-Avila:** Writing – review & editing. **Olivier Honnay:** Conceptualization, Funding acquisition, Project administration, Writing – review & editing. **Patricia Krickl:** Formal analysis, Project administration, Writing – review & editing. **Jan Plue:** Conceptualization, Writing – review & editing. **Peter Poschlod:** Conceptualization, Funding acquisition, Writing – review & editing. **Anna Traveset:** Conceptualization, Funding acquisition, Writing – review & editing. **James M. Bullock:** Conceptualization, Supervision, Writing – original draft.

Declaration of competing interest

The authors declare no conflict of interests. The work is all original research carried out by the authors. All authors agree with the contents of the manuscript and its submission to the journal.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2021.109152.

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