

Soil phosphorus availability determines the contribution of small, individual grassland remnants to the conservation of landscape-scale biodiversity

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Funding information

Jan Plue held a Future Research Leader grant by FORMAS (nr 2018-00961). The sampling campaign was supported by the Ghent University Research Fund (BOF).

Co-ordinating Editor: Viktoria Wagner

Abstract

Questions: Small, remnant habitats embedded in degraded, human-dominated landscapes are generally not a priority in conservation, despite their potential role in supporting landscape-scale biodiversity. To warrant their inclusion in conservation management and policy, we question under which conditions they may exhibit the largest conservation value.

Location: Nine landscapes spread across the counties of Stockholm and Södermanland, Sweden.

Methods: Per landscape, plant communities were surveyed in 6 and 12 $1 \times 1 \text{ m}^2$ plots across large, intact semi-natural grasslands and small remnant grasslands, respectively. These two contrasting grassland types served as a model system. A top-soil sample was taken in each plot to determine habitat quality in terms of soil pH, plant-available P, and C:N ratio. We used a joint species distribution model to analyse the extent to which grassland type and habitat quality define and predict resident community diversity and composition, including whether they support grassland specialists.

Results: At the landscape scale, the combined remnant grasslands sustained diverse plant communities which did include a significant subset of habitat specialists. Yet, the contribution of individual remnants clearly varied with local-scale habitat quality; soil phosphorus availability lowered plot-level species richness, mostly by constraining the occurrence of grassland specialists. Semi-natural grassland communities were comparatively insensitive to variation in soil phosphorus availability.

Conclusions: The combined habitat amount and the significant number of habitat specialists sustained by remnant grasslands with high habitat quality, shows they can represent a valuable resource to support landscape-scale biodiversity conservation. This offers no wildcard to neglect the continued biotic and abiotic threats on semi-natural grassland plant diversity such as chronic and accumulating P eutrophication, discontinuation of management or poor matrix permeability, as semi-natural

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grasslands harbour the majority of habitat specialists, while sourcing surrounding remnant grassland communities.

KEYWORDS

grassland specialists, joint species distribution models, landscape ecology, plant-available phosphorus, remnant habitats, semi-natural grasslands, species richness

1 | INTRODUCTION

The human footprint on the natural world has become globally pervasive, with over half of the terrestrial land area already being converted to human-dominated land uses and 75% of the terrestrial biosphere subject to measurable environmental pressures (Venter et al., 2016; Watson et al., 2016). These anthropogenic pressures are at the core of the ensuing global biodiversity crisis (Haddad et al., 2015; Newbold et al., 2015). Protective habitat conservation measures, while effective (Gaston et al., 2008), fail to keep track, allowing habitat destruction outside of conservation areas to continue relentlessly (Halpern et al., 2015; Watson et al., 2016; Ridding et al., 2020). Consequently, bold nature retention goals should be set that go beyond the protected areas if biodiversity and its associated benefits for human society are to be conserved (Maron et al., 2018).

While global diversity declines are not easily translated to local scales (Dornelas et al., 2014; Vellend et al., 2017), immediate and delayed losses of biodiversity at landscape scales in response to land use change are widely accepted, across levels of biodiversity, across taxa, and across biomes (Essl et al., 2015; Halley et al., 2016). This is also true for grassland conservation in European agricultural landscapes, for which landscape-scale biodiversity hinges upon functioning networks of remaining (semi-)natural habitats, a task often bestowed upon large, extensively managed and unimproved semi-natural grasslands (Öckinger & Smith, 2007; Billeter et al., 2008). Traditionally managed, semi-natural grasslands hold high ecological value, sustaining exceptional plant and animal diversity (Wilson et al., 2012), as well as a suite of ecosystem services (Bengtsson et al., 2019). Still, these poorly protected grasslands are a non-profitable, obsolete component of modern agricultural production (Kumm, 2004), which has driven their sustained and still ongoing decline over the past 150 years (Cousins et al., 2015; Auffret et al., 2018; Ridding et al., 2020). Significant negative impacts on biodiversity and related ecosystem services have consequently been repeatedly confirmed across European agricultural landscapes (Krauss et al., 2010; Bullock et al., 2011; Cousins et al., 2015).

In order to attain nature retention goals, conservationists are increasingly turning their attention to small, remnant or even artificial habitats that are scattered in the landscape to assess their potential in conserving biodiversity in human-dominated landscapes (Wintle et al., 2019). These include, for example, urban lawns (Thompson et al., 2004), small forests (Valdés et al., 2019), burial mounds (Deak et al., 2018), hedgerows (Staley et al., 2013), ditches (Meier et al., 2017), forest edges (Lindgren et al., 2018), road verges (Auffret &

Lindgren, 2020) or other linear landscape features (Gardiner et al., 2018). Such small, individual habitat patches tend to support only a limited number of species, yet their combined surface area can substantially contribute to the landscape-scale habitat amount (Lindgren & Cousins, 2017; Gardiner et al., 2018), potentially increasing the species density in local communities (Watling et al., 2020) and harbouring important portions of landscape-scale species pools, including habitat specialists (Deak et al., 2018; Gardiner et al., 2018). Furthermore, the small habitat patches significantly increase landscape matrix permeability, enhancing the dispersal and movement of species (Auffret et al., 2017b; Gilbert-Norton et al., 2010), and helping to maintain viable meta-communities between large, semi-natural habitat patches (Sullivan et al., 2017; Damschen et al., 2019, but see Saura et al., 2013). Yet, the fact that the ecological value of small remnant habitat patches is disproportionate to their size, is insufficiently recognised, so that they are deprioritized in conservation policy, planning and management (Poschlod & Braun-Reichert, 2017; Fahrig, 2019).

To better inform biodiversity conservation management about the value of remnant habitat patches, some warranted questions regarding their ecological value and conservation status need to be resolved. These include, among others, whether time lags in local extirpations may explain their high species richness (Cousins, 2006), if their small populations are sinks within meta-population dynamics, rendering them dependent on the presence of large habitat patches (Harrison 1991, but see Altermatt & Ebert 2010), or if they actually make an effective contribution to functional connectivity (Saura et al., 2013). Here, we will focus on the extent to which habitat quality, in terms of soil abiotic conditions, defines and predicts resident community diversity and composition, including the degree to which they support habitat specialists. Habitat quality is of critical importance for the long-term survival and persistence of numerous grassland (specialist) species relative to other landscape and management factors (Gonthier et al., 2014; Zulka et al., 2014; Gilhaus et al., 2017; Milberg et al., 2020). Elevated nutrient status in general, and N and P levels in particular, are well known to decrease grassland biodiversity in grasslands across Europe (Duprè et al., 2010; Ceulemans et al., 2013, 2014; Humbert et al., 2016), mostly by reducing the occurrence of individual grassland (specialist) species (Gilhaus et al., 2017). The high edge/area ratio of small remnant habitat patches compared to intact grassland habitat entails that core, high-quality habitat is frequently absent (Ries et al., 2004), due to detrimental edge effects (e.g. the influx of fertilisers) entirely encompassing the patches (Hofmeister et al., 2013). The synergy between small patch size

and nutrient influx from the surrounding intensively used matrix will thus likely exert a detrimental impact on local habitat quality, in turn degrading community species richness and composition (Ewers et al., 2007), largely related to the loss of habitat specialists (Cachovanová et al., 2012).

Our study system is the plant communities of large semi-natural grasslands spread across nine fragmented agricultural landscapes in Central Sweden. We compare semi-natural grassland communities with the plant communities of unmanaged, remnant grassland habitat patches found on midfield islets occurring throughout the agricultural matrix in these landscapes. We use plant communities as model system as plant extinctions are likely to induce extinction cascades throughout trophic ecological networks (Schleuning et al., 2016). We aim to address the following research questions: (a) do the remnant grassland plant communities support a relatively high landscape-scale plant species diversity, which is disproportionate to the habitat amount they represent in these fragmented landscapes; (b) to what extent does the soil abiotic environment predict local-scale plant species diversity in large vs remnant grassland communities; (c) how do the individual species and, ultimately, the community composition change along gradients in the soil abiotic environment;

and (d) what is the relative importance of grassland type (semi-natural grassland or remnant grassland) vs the soil abiotic conditions in controlling the community patterns?

2 | METHODS

2.1 | Study area

We thus set out to assess how abiotic conditions shape the plant communities of remnant grassland habitats and, as such, the potential contribution of these remnant communities to conserve plant species richness in agricultural landscapes, relative to large, intact semi-natural grasslands. We therefore selected a suite of nine landscapes which contain fragments of semi-natural grasslands, spread across the counties of Stockholm and Södermanland, Central Sweden (centroid at 58.930° N, 17.085° E; Figure 1a, Table S1). Each landscape was centred around a large, grazed and unimproved semi-natural grassland, which was largely isolated from other large semi-natural grasslands (by at least 1.5 km) and surrounded by an intensively used silvi- and agricultural matrix. A circular landscape

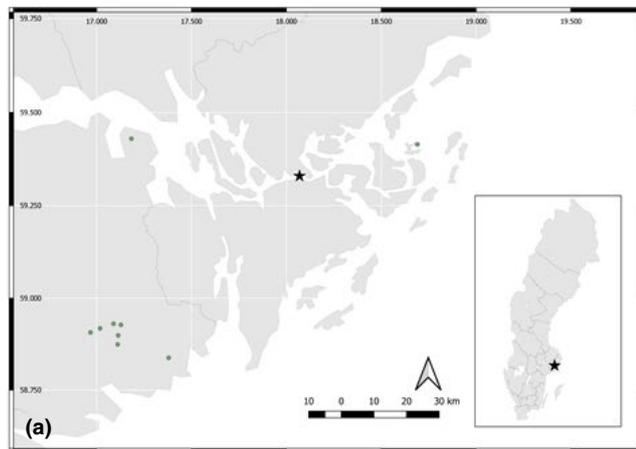


FIGURE 1 Geographical location of the nine sampled landscapes (green dots; star = Stockholm) in Central Sweden (a). Per landscape, grassland plant communities were inventoried in six remnant grassland communities located on midfield islets embedded in arable fields (two 1 m × 1 m plots per remnant) as well as in a nearby, large and intact semi-natural grassland (six 1 m × 1 m plots; blue dots), as demonstrated for the landscape at Uppsala kulle (b). Photos illustrate the small, remnant grasslands embedded in an agricultural matrix in the landscape at Överselö (c), whereas (d) represents a typical, species-rich semi-natural grassland sampled in the landscape at Aspa

with a 3-km diameter was delineated around each focal semi-natural grassland, and we randomly selected a series of six so-called mid-field islets in the surrounding landscape (Figure 1b). These are unmanaged, small remnant grassland habitat patches typically dotted across Swedish agricultural landscapes. They are nowadays embedded within arable fields or old-fields, and many have a history of grazing management. They usually consist of either large stones and boulders or bedrock impediments covered by a thin soil layer, which renders them unsuitable for agriculture. Although recurrent drought often slows down woody encroachment (Cousins, 2006), an open tree canopy can develop (Plue & Cousins, 2013). Midfield islets hence provide a marginal grassland habitat where grassland (specialist) species may survive (Cousins & Lindborg, 2008; Plue & Cousins, 2013; Lindborg et al., 2014). They can vary substantially in size, and selected mid-field islets in this study had a mean size of 1,865 m² (standard error [SE] ± 170 m²) and ranged between 190 m² and 7,579 m² in area. For comparison, the nine focal semi-natural grasslands had a mean surface area of 115,550 m² (SE ± 40,492 m²; range 19,333–390,246 m²). From here onwards, we will refer to the mid-field islets as remnant grasslands.

2.2 | Data collection

Within each of the nine landscapes, we recorded all plant species occurrences in a total of 18 1 m × 1 m vegetation plots between June and August 2018. Six plots were randomly scattered throughout the focal semi-natural grassland to get a comprehensive overview of the grassland plant community, as supported by starting saturation in the species–area curves for each of the nine focal semi-natural grasslands (Figure S1). In each of the six selected remnant grasslands, we recorded the plant communities in two separate plots, one positioned in the centre and one near the edge, for a total of 12 plots per landscape. The total number of vegetation plots was 162. All recorded plant species were classified into two ecological groups identifying their habitat specialisation, for further use in the data analyses. Grassland specialist species (e.g. *Polygala vulgaris* and *Briza media*) are those species which decline rapidly within 5–10 years after grassland management has stopped. All other recorded species are considered non-specialist grassland species (e.g. *Galium verum* and *Agrostis capillaris*), ranging from ruderal over grassland generalists to light-dependent forest species. This classification is based on the grassland species indicator list (based on their management dependence) developed for Swedish grasslands and meadows by Ekstam and Forshed (1997), a list frequently used to identify Swedish grassland specialists (e.g. Plue & Cousins, 2013; Lindborg et al., 2014; Lindgren & Cousins, 2017). Though eight red-listed species were recorded in both semi-natural and remnant grasslands (Table S2; SLU Artdatabanken, 2020), this species subset (eight out of a total of 174 recorded species) was too limited to execute a reliable statistical analysis set to acutely ascertain the value of remnant grassland for species of the highest conservation concern.

In each vegetation plot, we took five mineral topsoil (0–10 cm) samples with a gouge auger to characterise the soil abiotic environment. For more superficial soils (<10 cm soil depth), we sampled the maximum depth possible. The five plot-level samples were pooled into one composite soil sample per plot in the field. Then, we performed wet-lab measurements of the soil pH (soil acidity), C/N ratio (indicator of soil fertility and soil biological activity such as mineralisation and decomposition) and plant-available phosphorus (P; indicator of eutrophication due to agricultural activities). Prior to processing, all soil samples were dried to constant weight at 40°C for 48 hr and then ground and sieved (2 mm mesh) after removing the coarse plant and organic material. Analyses for soil acidity (pH-H₂O) were done by shaking a 1:5 ratio soil/H₂O mixture for 5 min at 300 rpm and measuring with a pH meter Orion 920A with pH electrode model Ross sure-flow 8172BNWP (Thermo Scientific Orion, Waltham, USA). The C/N ratio was quantified by combusting each individual soil sample at 1,150–1,200°C and the gases were measured by a thermal conductivity detector in a CNS elemental analyser (vario Macro Cube, Elementar, Langensfeld, Germany). Finally, plant-available P (i.e. available for plant growth during the growing season; Gilbert et al., 2009) was extracted by NaHCO₃ (P_{Olsen}; according to ISO 11,263:1994[E]) and measured colorimetrically according to the malachite green procedure (Lajtha & Jarrel, 1999). Phosphorus concentrations are expressed as mg P kg⁻¹ dry soil.

2.3 | Data analysis

2.3.1 | Landscape level

To assess landscape-scale species richness patterns, we first calculated the total number of species found across the plots in the semi-natural or remnant grasslands of each landscape. To account for the difference in the number of vegetation plots sampled in the semi-natural grasslands ($n = 6$ per landscape) and remnant grasslands ($n = 12$ per landscape), the species richness of the remnant grasslands needed to be rescaled. We calculated the average number of species across six plots, through sample-based rarefaction ($n = 100$ permutations). Then, we determined whether differences in richness between semi-natural grasslands and remnant grasslands are largely due to the total habitat amount or, conversely, that the richness in remnant grasslands is disproportionate to the habitat amount they represent (research question a). Here, we used the total area of the semi-natural grassland or the sum of the areas of the sampled remnant grasslands in each landscape as a measure of habitat amount (expressed in hectares). First, we compared the log-transformed habitat amount between semi-natural and remnant grasslands (effect of grassland type), using a hierarchical model with a group-level effect for landscape, so that the effect of grassland type was tested within landscapes. Second, we tested the relationship between the (rarefied) landscape-scale species richness and habitat amount and the difference in this relationship between the two grassland types. We used a hierarchical model again, with habitat amount (log-transformed

and mean-centred), grassland type, and their interaction as predictors and a group-level effect for landscape. Third, we fitted the same model, but without habitat amount as predictor, i.e. simply comparing richness between grassland types within landscapes. The same model was fit on the full data set, the subset of data only including the grassland specialist species, and the subset of data only including the non-specialist species. Models were fitted using the linear mixed-effects models function in the *nlme* R package (Pinheiro et al., 2019).

2.3.2 | Plot level

Plot-level changes in the species richness of the plant communities along abiotic gradients in soil pH, C/N and P were quantified with hierarchical models. Specifically, we tested whether the relationship between the species richness and the soil properties in the 1-m² vegetation plots differed between the semi-natural and remnant grasslands (effect of grassland type; research question b). Predictor variables were thus soil pH, C/N, P (all mean-centred) and grassland type, including the interaction terms between the soil abiotic variables and grassland type. To account for the spatial non-independence of observations within landscapes and plots within the same habitat patch (semi-natural or remnant grassland), the hierarchical models included group-level effects for landscape and patch ID nested within landscape. The response variable species richness was natural log-transformed. The same model was fit on the full data set, the subset of data only including the grassland specialist species, and the subset of data only including the non-specialist species.

The variation in community composition along the same abiotic gradients and the dependency of these patterns on grassland type (semi-natural vs remnant grassland; research question c) was quantified within the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et al., 2017). The modelling framework is based on joint species distribution models, that is, statistical models for the abundance (here presence/absence) of multiple species accounting for the correlation between these species as well as their response to predictor variables (Warton et al., 2015). We further refer to this model as the “species community model.” Essentially, we fitted the same model that was used for the plot-level species richness analysis, but now with the full plot × species presence/absence matrix as the response. Predictors were thus the abiotic variables (pH, C/N, and P) and grassland type, again including an interaction between each of the abiotic variables and grassland type. Landscape and patch ID were also the group-level effects here. In addition to the plot-level scale variables, we also included a species-level scale predictor in the model: the grassland specialist vs non-specialist indicator. This way, the model tests the influence of the specialisation of species on their occurrences along the abiotic gradients and grassland types (i.e. a fourth-corner approach). The model was fitted using the *Hmsc* R application (Tikhonov et al., 2019). We used the probit family (with log-link function) as the observation model for the species occurrence data. Sample settings: running two independent Markov chain Monte Carlo (MCMC) chains,

executing 500 MCMC steps before recording posterior samples (transient steps), recording 1,000 samples per chain, and taking 10 steps between each recording of samples from the posterior (thinning). Convergence of the model was checked based on the effective sample size (>500) and the Gelman–Rubin diagnostic (potential scale reduction factor [PSRF] close to one) of all parameters. The model fit is given by an R^2 value for each species. The different model parameters allowed to visualise and make inferences about the individual species’ responses along gradients in the predictors, the degree to which these responses are influenced by the species’ specialisation to grasslands, and the proportions of variance explained by groups of predictor variables (soil properties, grassland type, and the spatial-context variables landscape and patch; research question d).

All data analyses were done in R 3.6.2 and graphs were created with the *ggplot2* package (R Core Team, 2019; Wickham, 2016). R scripts for data preparation and statistical analyses are deposited at the Figshare online repository (Plue & Baeten, 2021).

3 | RESULTS

3.1 | Landscape level

The semi-natural grasslands were on average 11.6 ha in surface area, whereas the sum of the areas of the remnant grasslands was on average 1.1 ha (Figure 2). This difference in habitat amount of the two grassland types was statistically significant ($p < 0.001$). There was no significant relationship between habitat amount and landscape-scale species richness within grassland types (all species, grassland specialist, non-specialists; all $p > 0.1$; Figure 2). A simple comparison of species richness between the grassland types, i.e. without controlling for habitat amount as covariate, showed that there were significantly more specialist species found in the semi-natural grasslands (average, 25.4 species across six 1-m² plots) compared with the remnant grasslands (average, 15.6; $p = 0.002$; Figure 2b). The two grassland types were not different in terms of all species (Figure 2a) or the non-specialist species (Figure 2c).

3.2 | Plot level

The mean plot-level plant species richness was higher in semi-natural grasslands (23.9 ± 1.2 SE) compared with the remnant grassland (15.7 ± 0.6 SE). Among the abiotic soil variables, only gradients in plant-available soil P showed a relationship with the total species richness (Figure 3a); the variation in richness was not related to soil pH and C/N (Figure S2 in the Supplementary Material). Furthermore, the influence of P differed between the two grassland types: while the total plant species richness was not related to the P in semi-natural grasslands (slope parameter $t = -0.9$; $p = 0.35$), the trend in remnant grasslands was significantly more negative (P × remnant grassland effect $t = -2.1$; $P = 0.04$). This decline in richness with increasing soil P in remnant grasslands was mainly driven by the loss

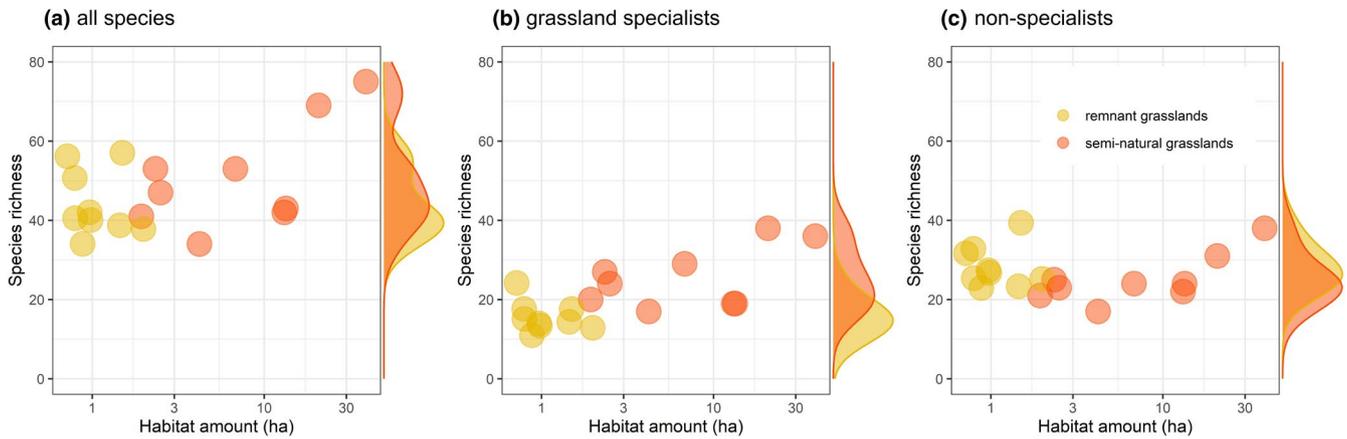


FIGURE 2 Landscape-level species richness patterns in relation to habitat amount for (a) all species, (b) the subset of grassland specialists and (c) the subset of non-specialist species. There was no significant relationship between habitat amount and richness. Differences between the grassland types, without accounting for habitat amount as a covariate (density curves along y-axis), showed only a significant difference for grassland specialists. Species richness is the total number of species found across the plots in the semi-natural or remnant grasslands of each landscape. The habitat amount represents the total area of semi-natural grassland or the sum of the areas of the sampled remnant grasslands in each landscape. To account for the difference in the number of vegetation plots between semi-natural grasslands ($n = 6$ per landscape) and remnant grasslands ($n = 12$ per landscape), the species richness of the remnant grasslands was rescaled to the average richness found in six plots (rarefaction)

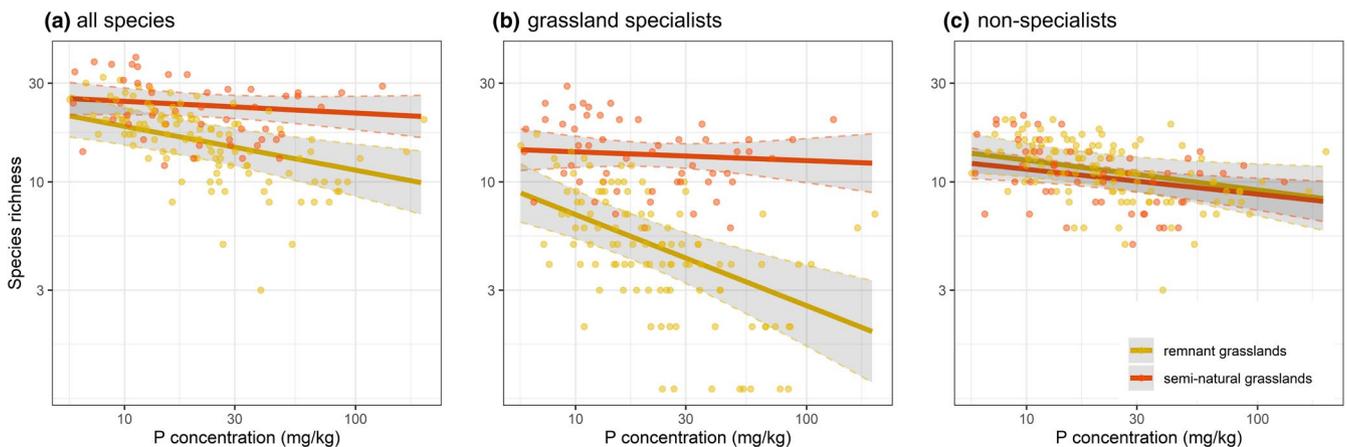


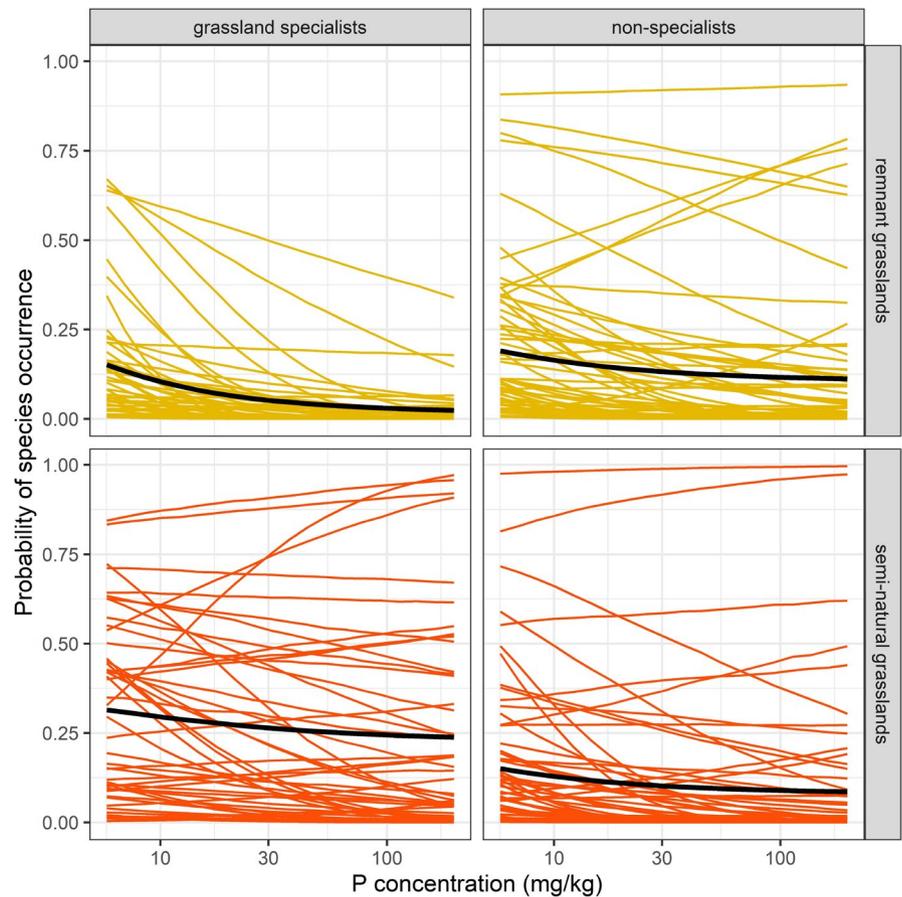
FIGURE 3 Changes in plot-level species richness along a gradient in bioavailable soil phosphorus concentrations for (a) all plant species, (b) the subset of grassland specialist species, and (c) the subset of non-specialist species. Data are shown along log-transformed scales. Lines show predicted trends ($\pm 95\%$ confidence interval [CI]) for semi-natural grasslands vs remnant grasslands that were derived from hierarchical models. The conditional coefficient of determination was $R^2 = 0.72$ (all species), $R^2 = 0.74$ (specialists), and $R^2 = 0.50$ (non-specialists). See main text for model specification and Figure S2 for richness changes along gradients in soil pH and C/N

of grassland specialists (Figure 3b); the richness of non-specialist species did not show a clear relationship with plant-available soil P ($t = -1.9$; $p = 0.06$).

The species community model had a median species-level fit $R^2 = 0.17$ (Tjur's coefficient of determination), with the first and third quartile equal to 0.09 and 0.28, respectively. Species occurrence patterns of grassland specialists along a gradient in soil P were clearly different between the two grassland types (Figure 4, left column; Figure S4). While specialist species generally decreased with increasing P in the remnant grassland communities, several maintained a similar occurrence probability along the P gradient in semi-natural grasslands (e.g. *Campanula rotundifolia* and *Festuca*

ovina; Figure S4). This is also seen in the model parameters expressing how the specialisation of species influences their environmental responses: for specialist species, we found no association with soil P in semi-natural grasslands and a negative association with soil P in the remnant grasslands (Figure S3). These species-level patterns are consistent with the contrasting changes in the species richness of specialists in the two types, that is, richness only decreased with soil P in the remnant grasslands (Figure 3b). The non-specialist species did not show clearly different patterns along the P gradient in the two grassland types (Figure 4 right column; Figure S4). The effect of the other two abiotic soil variables on specialist species also differed between grassland types: increases in occurrence with increasing

FIGURE 4 Compositional changes over gradients in bioavailable soil phosphorus concentrations. Lines represent predicted changes in the probability of occurrence of individual grassland specialist species (left column) or individual non-specialist species (right column) in remnant grasslands vs semi-natural grasslands (rows). The thick black lines represent the average across the species responses. Figure S4 contains a number of examples on the predicted changes in the probability of occurrence of individual grassland species, both specialist and non-specialist. Each line is derived from the same species community model, using a constructed gradient in soil P in the two grassland types, keeping the other abiotic variables at constant values; here predictions are for soils with average C/N ratio and high soil pH (90% quantile of observed pH values; pH = 6.01). Similar species responses along a C/N and pH gradient are shown in Figure S5



soil pH and soil C/N ratio were mainly found in semi-natural grasslands; in remnant grasslands occurrences generally remained low across the entire pH and C/N range (Figure S5). Non-specialist species show little consistent responses to soil pH and C/N (Figure S5).

Soil abiotic variables explained proportionally most of the variation in community patterns in semi-natural grasslands (Figure 5a). Communities were not clearly differentiated between the particular landscapes or patches within those landscapes. The grassland type effect was also small. The strong variation in probability of occurrence between species therefore provides little information when one wants to predict the probability a species is present in a sampled semi-natural grassland plot. The same trends were found for both the grassland specialist and non-specialist species. In the remnant grasslands, the relative contribution of soil gradients to the community patterns was lower (Figure 5b). Now, the effect of grassland type became more important. In other words, when a plot was located in a remnant grassland, this fact was relatively informative for predicting individual species absences.

4 | DISCUSSION

This study adds to the growing body of evidence that small, remnant habitats can sustain diverse plant communities. Together, the remnant grassland patches in a landscape represented an important source of biodiversity, supporting a substantial part of the specialist species

pool (see also Deak et al., 2018; Gardiner et al., 2018). Yet, not all individual remnant grasslands contributed equally to this landscape-level diversity. High soil phosphorus availability constrained the probability of habitat specialists finding a suitable habitat in individual remnant habitat patches, lowering their individual species richness (Ries et al., 2004; Ewers et al., 2007) and amplifying the already negative impacts of habitat loss and fragmentation per se (Chase et al., 2020). When one aims for a continued contribution of remnant grasslands to plant diversity in degraded human-dominated landscapes, in addition to the protection and conservation of large, intact habitats (Hodgson et al., 2011), safeguarding their habitat quality is key.

4.1 | Habitat quality effects differ between grassland types

The soil abiotic environment clearly influenced patterns in the plant community diversity and composition, especially for the group of grassland specialist species. More specifically, we found increasing plant-available soil P concentrations to induce plant community disassembly, with a logarithmic decline of species richness in the remnant plant communities (range of 5.8–197.5 mg P kg⁻¹; plant-available P_{Olsen}), driven predominantly by the loss of grassland specialist species (Ceulemans et al., 2011; Figure S4). European semi-natural grasslands have indeed shown rapid logarithmic declines in species richness up to concentrations of ~120 mg P kg⁻¹, after which species

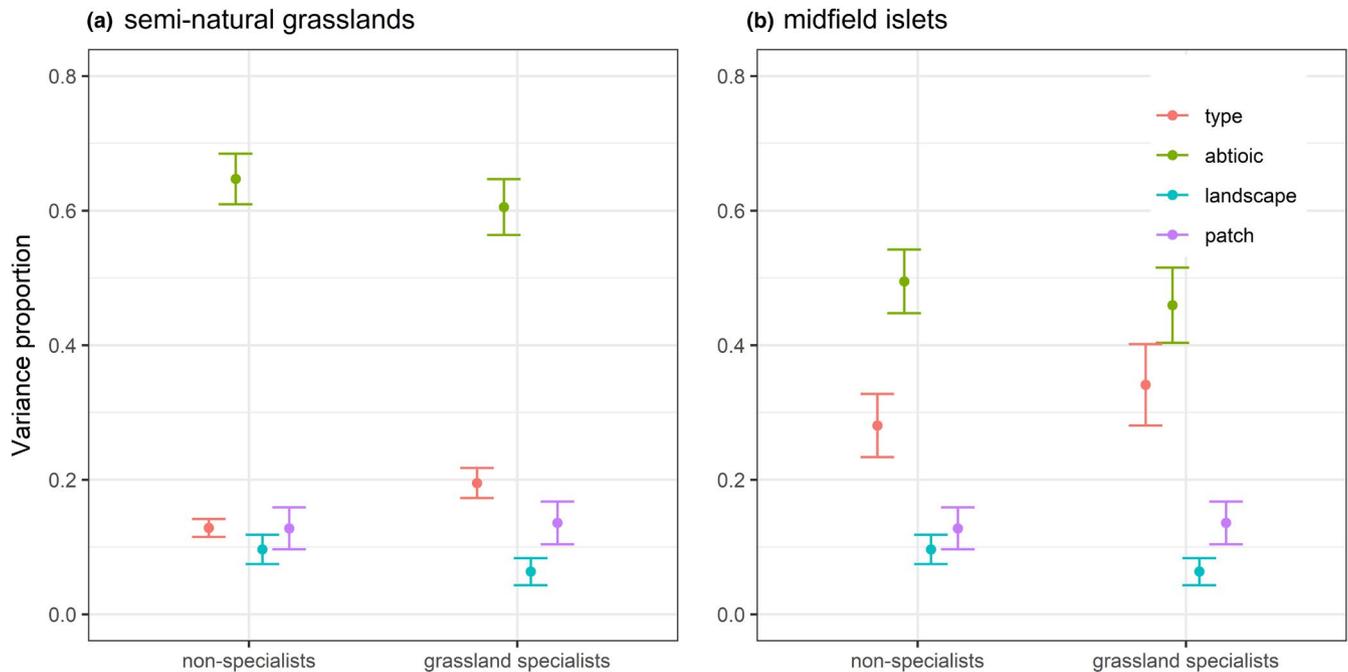


FIGURE 5 Proportion of variance explained by groups of predictor variables in the fitted species community model. The type component refers to the habitat type effect in the model, that is, the degree to which being in a semi-natural grassland or remnant grassland explains the average probability of occurrence of the species. The abiotic component summarizes how much species occurrences are explained by soil P, pH, and C/N ratio. The landscape and patch components express the degree to which species' occurrences are linked to their presence in particular landscapes or patches within landscapes (i.e. semi-natural grassland or individual remnant grassland patches). Variance components are available at the species level and are here summarized (mean \pm 95% confidence interval [CI]) for grassland specialist vs non-specialist plant species

richness stabilises (Ceulemans et al., 2014). As for our semi-natural grasslands, they showed a similar range in plant-available soil P (6.0–130.6 mg P kg⁻¹) compared to that in Ceulemans et al., (2014) as well as the sampled remnant communities, but neither the total nor specialist species richness showed a clear decline.

The similar levels of elevated soil P levels in both remnant and semi-natural grasslands are a likely consequence of spill-over effects of P fertilisation on the surrounding arable fields. Yet, plant communities did not respond similarly, suggesting that the differences in the relative importance of soil P between grassland types may be related to clear differences in patch size and grassland management. Indeed, the larger patch sizes of semi-natural grasslands likely support higher small-scale soil heterogeneity, helping specialist species to evade unsuitable microhabitats suffering from high P availability, ultimately enabling their local persistence (Chesson, 2000). Grassland management may offer an added, complementary explanation. Remnant grasslands are generally unmanaged so that generalist species, often being more competitive species (Boulangeat et al., 2012), can respond rapidly to P eutrophication by vigorous plant growth. They may then gain dominance in the community and outcompete stress-tolerant, low-statured and slow-growing grassland specialists as their rapidly extending herbaceous canopy deprives these specialists of light (Duprè & Diekmann, 2001; Hautier et al., 2009; Ceulemans et al., 2011; Auffret et al., 2017a). The continued grazing management of semi-natural grasslands, on the other hand, keeps elevated P-induced biomass production in check (Duprè & Diekmann, 2001),

and maintains grassland habitat heterogeneity (Dirzo et al., 2014), crucial for the establishment and persistence of grassland specialists (Figure 4; Bullock et al., 1994; Kapás et al., 2020). Management may thus maintain high grassland species richness despite P eutrophication. Moreover, this strong grazing control allows individual species and (specialist) species richness of semi-natural grassland communities to be primarily governed by other important abiotic soil conditions such as soil pH and soil C/N (Figure S5; Stevens et al., 2010).

4.2 | Importance of remnant grasslands for conservation

Individual remnant grassland communities are thus subject to strong control of habitat quality, (Gonthier et al., 2014; Zulka et al., 2014), most likely due to the synergetic interaction between their small size, isolation and nutrient influx (Ries et al., 2004; Ewers et al., 2007). Yet, we also found that, as a group, they can support a similar amount of plant species richness as a semi-natural grassland, including an important number of grassland specialist species (Lindborg et al., 2014; Deak et al., 2018; Gardiner et al., 2018). Moreover, at only a fraction of the surface area of semi-natural grasslands, this seems to affirm that their value for biodiversity conservation and policy may indeed have been underestimated (Poschod & Braun-Reichert, 2017; Fahrig, 2019; Wintle et al., 2019). This is particularly true, considering that their contribution

likely depends on an even smaller subset of high-quality, low-P remnant grasslands. Though this may give rise to justifiable optimism, two significant concerns remain regarding their ecological function, value and opportunities towards biodiversity conservation.

First, remnant grassland fragments form a vital part of a landscape's green infrastructure, i.e. the assemblage of structural elements of (remnant) semi-natural habitats, structurally connecting large, remaining semi-natural habitats (Kimberley et al., 2020). However, their mere presence does not guarantee that plant species migrations are effectively happening along these remnant grasslands, supporting so-called functional connectivity (Auffret et al., 2017b). Numerous environmental factors such as matrix quality, management or habitat age indeed constrain the efficiency of the green infrastructure (Baum et al., 2004; Aavik & Liira, 2010; Thiele et al., 2018; Auffret & Lindgren, 2020), and our results add habitat quality of the remnants prominently to this list. Local habitat quality has repeatedly been pinpointed as a crucial factor explaining the richness and abundance of numerous taxa when compared to other patch- and landscape-scale variation in large, intact semi-natural grasslands (Gonthier et al., 2014; Zulka et al., 2014), but it is clear from our results that this also holds for the grassland remnants. Our results therefore suggest that remnant communities may potentially not contribute to functionally connecting remaining semi-natural grasslands for grassland specialists (Beier & Gregory, 2012; Saura et al., 2013). Indeed, high-quality, low-P habitat is likely absent within numerous remnant grasslands, implying that only a subset of remnant grasslands may be effectively contributing to support a landscape's functional connectivity. Consequently, dispersal and recruitment opportunities between high-quality remnant grasslands and semi-natural grasslands are reduced further in a species group with trait syndromes typically already indicative of poor dispersal capabilities (Saar et al., 2012; Auffret et al., 2017a; Thiele et al., 2018). This is particularly problematic, as increasing levels of green infrastructure which supposedly enhance the landscape's permeability are still failing to offset continued losses of semi-natural grasslands (Kimberley et al., 2020).

A second major concern is the elevated P status of the remaining semi-natural grasslands, upon which landscape-scale biodiversity is primarily dependent (Öckinger & Smith, 2007; Billeter et al., 2008). Without proper grazing management, high P levels can be expected to quickly depress their biodiversity, as the strongest species losses already occur at small increases in soil P (Ceulemans et al., 2014), notably due to rapidly ensuing extirpations of grassland specialists (<5 years; Ekstam & Forshed, 1997). This raises the central question to what extent remnant communities support diverse plant communities in the absence of large, intact semi-natural grasslands. Lindgren and Cousins (2017) pinpointed that island biogeography is a better model than habitat amount to predict the presence of grassland specialists on remnant grassland communities identical to those studied here. Combined with the comparatively higher likelihood of grassland specialists being absent from remnant communities regardless of soil conditions, this suggests source/sink dynamics are at

work within the landscape's metacommunity (Pulliam, 1988; Holyoak et al., 2005; Hodgson et al., 2011). One could imagine large source populations of grassland specialists in the semi-natural grasslands to support an outward flow of migrants, leading to some grassland specialists successfully establishing in remnant grassland communities, which then represent sink communities given their suboptimal to poor habitat quality. If so, this would explain why individually impoverished remnant grassland communities as a group may still support diverse plant communities with numerous specialists. At the same time, it highlights their possible vulnerability if source populations disappear. Consequently, the ecological and functional value of these remnant communities for biodiversity conservation may very well hinge upon the presence of large, well-managed semi-natural grassland communities. At least a subset of high-quality, remnant grasslands currently still support a diverse suite of grassland species which can be wielded to help conserve landscape-scale biodiversity if grassland management is re-instated (Cousins & Lindborg, 2008).

Measures rehabilitating soil quality following chronic P eutrophication are a prerequisite for the recovery of grassland communities, but they demand a substantial and sustained effort which is often not feasible nor practical to implement (Schelfhout et al., 2015), particularly in small, isolated remnant grasslands. At the same time, P fertiliser applications continue at levels detrimental to biodiversity (Ceulemans et al., 2014) and large, intact semi-natural grasslands continue to be lost at alarming rates (Watson et al., 2016; Auffret et al., 2018; Kimberley et al., 2020; Ridding et al., 2020). Consequently, the protection and integrated landscape-scale management of semi-natural grasslands in agricultural landscapes must remain a top priority, in conservation management and policy actions (Hodgson et al., 2011; Watson et al., 2016). Still, in that arena, the ecological function, value and opportunities such as increased habitat area and functional connectivity provided by remaining, high-quality remnant grassland communities should be quantitatively recognised, in order to appreciate that these communities continue to suffer the same threats as semi-natural grasslands. If not, besides degrading the ecological functioning of the landscape's green infrastructure, failure to address the detrimental synergy between habitat loss and habitat quality at the landscape scale consequently risks the degradation of biodiversity manifesting itself to its full extent (Chase et al., 2020).

ACKNOWLEDGEMENTS

We acknowledge Sara A.O. Cousins in her capacity of PI of the FUNgreen project (BiodivERsA – 2015–2016 COFUND call), the baseline for this satellite project, and for comments on an earlier draft of the manuscript. The authors are grateful for the fieldwork by Delphine Parmentier, assisted by Rozalia Kapas. JP held a Future Research Leader grant by FORMAS (nr 2018-00961). LB was supported by the Ghent University Research Fund (BOF).

AUTHOR CONTRIBUTIONS

Both authors conceived, designed and wrote the paper. JP collected the data while LB analysed the data.

DATA AVAILABILITY STATEMENT

All underlying geographical, soil, plant community and plant trait data and R scripts not available in the main manuscript or in Supporting Information are publicly available on Figshare (<https://figshare.com/>) at <https://doi.org/10.17045/sthlmuni.14614263>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Table S1. Location and descriptive statistics of the nine sampled landscapes in Stockholm and Södermanland counties in Sweden

Table S2. Frequencies and relative abundance in semi-natural and remnant grasslands for all species recorded in nine agricultural landscapes in Stockholm and Södermanland counties in Sweden

Figure S1. Species-area curves for each of the nine sampled semi-natural grasslands

Figure S2. Changes in total plot-level species richness along a gradient in soil pH and soil C/N ratio in remnant grasslands versus semi-natural grasslands

Figure S3. Graphical representation of the influence of the species' specialisation on their occurrences between the grassland types and along the abiotic gradients

Figure S4. Individual species responses over a gradient in bio-available soil phosphorus concentrations

How to cite this article: Plue J, Baeten L. Soil phosphorus availability determines the contribution of small, individual grassland remnants to the conservation of landscape-scale biodiversity. *Appl Veg Sci*. 2021;24:e12590. <https://doi.org/10.1111/avsc.12590>