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RESEARCH ARTICLE

Communities in infrastructure habitats are species rich but only partly support species associated with semi-natural grasslands

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Abstract

1. Biodiversity linked to traditionally managed semi-natural grasslands is declining, despite conservation efforts. At the same time, the area of novel grassland habitats along linear infrastructure, such as road verges and power line corridors, is increasing and in some regions surpass the area of semi-natural grasslands. An open question is to what extent these novel grasslands can complement or even replace traditionally managed grasslands as habitat for grassland species.
2. We compared the alpha (species richness) and beta (abundance-based dissimilarities) diversity of plants, bumblebees and butterflies among semi-natural pastures, verges of small and big roads, power line corridors and uncultivated field borders nested within 32 landscapes (2 × 2 km squares). Landscapes had either high or low road density and were with or without power line corridors. Across landscapes there was also a gradient in the area of semi-natural pastures.
3. Alpha diversity of all three species groups was as high in power line corridors and verges of small roads as in semi-natural pastures, regardless of landscape composition. Although all habitat types shared a large proportion of species, community composition differed among habitats for all three species groups. The beta diversity of plants and butterflies was driven primarily by the replacement of species (turnover), while the beta diversity of bumblebees was driven by a rarer occurrence of certain species in road verges (nestedness). This means that linear infrastructure habitats cannot fully replace the role of semi-natural grasslands for plant and pollinator diversity.
4. The area of road verges, power line corridors and semi-natural pastures in the landscape influenced community composition of plants and butterflies, but not the similarity in community composition among habitats within landscapes.
5. *Policy implications*. Although novel grasslands along linear infrastructures have high numbers of grassland species, they only support a part of the biodiversity found in traditionally managed semi-natural grasslands. Therefore, protecting and restoring semi-natural grasslands should continue to be a priority for the conservation of grassland biodiversity. However, especially in landscapes where the

area of semi-natural grasslands is low, road verges and power line corridors can be important habitats for a number of grassland plants and insects and should be managed to promote biodiversity.

KEYWORDS
alpha, beta, bumblebees, butterflies, diversity, plants, power lines, road verges

1 | INTRODUCTION

Traditional semi-natural grasslands in north-western Europe, that is, grasslands that are maintained by extensive mowing or grazing but are unaffected by fertilization, ploughing or seeding, are extremely species rich but have been largely converted to arable land or forests (Strijker, 2005). Despite conservation efforts, the area of traditionally managed semi-natural grasslands continues to decrease (Feranec et al., 2010). The remaining patches of semi-natural grasslands are typically small, fragmented and embedded in intensively managed landscapes (Cousins et al., 2015). This leads to declining abundances and local extinctions of species dependent on these grasslands, and proliferation of generalists in the landscape (Nielsen et al., 2019). This is a major concern, given that extensively managed grasslands are not only hotspots for biodiversity but also provide valuable ecosystem services such as pollination, carbon storage and climate mitigation, among others (Bengtsson et al., 2019).

In contrast to the continuing decline of semi-natural grasslands, the area of novel grassland habitats along infrastructure, that is, linear infrastructure habitats, is increasing globally. In some European countries the area of such linear infrastructure habitats is even larger than the total protected natural area of the country (Jeusset et al., 2016). Linear landscape elements can support population viability by increasing habitat area and aiding the dispersal of species in the landscape (Vanneste et al., 2020). Furthermore, novel grassland habitats such as power line corridors, road verges and forest clear-cuts can have a high number of plant and insect species, including many species typically associated with traditionally managed semi-natural grasslands (Berg et al., 2011; Bergman et al., 2020; Phillips et al., 2019). For example, plant communities in road verges had high levels of grassland specialist species (Auffret & Lindgren, 2020), and bumblebee diversity in power line corridors was comparable to semi-natural grasslands (Hill & Bartomeus, 2016). There is increasing societal and scientific interest in using linear infrastructure habitats for biodiversity conservation (Gardiner et al., 2018; Phillips et al., 2021). However, it remains unclear what proportion of all grassland species can use areas along infrastructure as habitat, that is if these novel habitats support the survival and reproduction of species associated with semi-natural grasslands (Villemey et al., 2018).

The total number of species in a region (gamma diversity, ϒ) is shaped by both local diversity (α-diversity) and by the variation in community composition among sites (β-diversity) (Whittaker, 1960). β-diversity among grassland types in a landscape can depend on differences in management (Oldén & Halme, 2016). In addition to management, the number and identity of species within each of these habitat types can depend on the patch size, neighbouring habitat, land-use history, habitat age and on the landscape structure and configuration (Auffret & Lindgren, 2020; Janišová et al., 2014; Öckinger & Smith, 2007a). β-diversity can also be shaped by dispersal of organisms, and hence by landscape connectivity. In landscapes with low connectivity, β-diversity is expected to be high because the community composition in isolated patches is mainly shaped by local factors, whereas dispersal can homogenize local communities when landscape connectivity is high (Tscharntke et al., 2012).

Patterns in α- and β-diversity can differ among species groups, depending on their life-history traits, such as dispersal capacity and niche breadth (Gómez-Rodríguez et al., 2015). For instance, plants typically respond slowly to environmental change, and extinctions and colonizations lag behind both the loss of habitat in the landscape (Kuussaari et al., 2009) and the creation of new habitats, such as road verges (Auffret & Lindgren, 2020). In contrast, mobile animals respond faster to environmental change and can also move among different habitat patches, which might make them less vulnerable to reduced habitat area (Öckinger et al., 2012). The dissimilarity in community composition is expected to be larger for more specialized species than for generalists (Dormann et al., 2007).

To understand how to best maintain biodiversity and guide conservation actions, we need to identify which habitats contribute to ϒ-diversity by exploring patterns in β-diversity (Ruhí et al., 2017; Santana et al., 2017). If β-diversity is driven primarily by nestedness, that is, species assemblages in species-poor habitats are a subset of the community in more species-rich habitats, then conservation of the richer habitat should be prioritized as well as the restoration of the poorest habitat. On the other hand, if β-diversity is primarily driven by turnover, that is, species replacements among habitats, conservation actions could focus on landscape management where, for example, improving landscape connectivity would be an appropriate approach (Santana et al., 2017).

We compared species richness and composition between traditionally managed semi-natural pastures and linear infrastructure habitats to assess the contribution of each habitat type to landscape-scale biodiversity for three groups of species that differ in mobility and habitat specialization: plants, butterflies and bumblebees. We compared α (species richness) and β-diversity (abundance-based dissimilarities) of these species groups among five grassland habitat types: power line corridors, road verges of big and small roads, semi-natural pastures and uncultivated field borders. We predicted that

(1) linear infrastructure habitats have as high α-diversity as semi-natural pastures, (2) α-diversity is affected by the amount of habitat, that is, land cover of semi-natural pastures, road verges and power line corridors, in the 4 km^2 landscape, (3) landscapes with a higher amount of linear infrastructure habitats have lower β-diversity than landscapes with a low amount due to increased landscape structural connectivity and (4) β-diversity among habitat types depends on the dispersal ability and the degree of habitat specialization within species groups, and hence be highest for plants and lowest for bumblebees.

2 | MATERIALS AND METHODS

2.1 | Study design

We investigated the effect of power line corridors, road verges and semi-natural pastures in the landscape on the diversity of plants, butterflies and bumblebees in five types of prevalent grasslands in landscapes with contrasting composition. We crossed the factors 'road verge density' and 'the presence of power line corridors' by selecting 32 landscapes of 4 km^2 each in south-east Sweden (Figure 1a). We selected landscapes to fit into four categories to achieve a crossed design (Figure 1b). Sixteen of the landscapes had at least one power line corridor while the other 16 did not, and 16 of the landscapes had a high road density while the remaining 16 had a low road density (Figure 1b). Road density was used as a proxy for the area of road verges in the landscape (Table S1). An average road verge width was calculated for road verges along big, paved roads (average width = 2.8 m, n = 31) and another for road verges along small gravel roads (average width = 2.9 m, n = 24). These values were multiplied by two (one for each side of the road), and the final values were used to calculate road verge area by multiplying them with the total road length in the landscape. Additionally, all four landscape categories had a gradient in the area (0.8%–9.9% of the total landscape area) of semi-natural pastures, independent of the area of linear infrastructure habitats. To select the landscapes, we created a 2×2 km grid over the counties of Uppsala, Stockholm, Södermanland and Västmanland in Sweden, and selected landscapes that had similar amounts of arable land and forest cover and that had contrasting amounts of linear infrastructure habitats (Figure S1). All landscapes were dominated by forest (mean forest cover = 63.4%, min = 45.2, max = 81.2, mean arable land cover = 20.9%, min = 1.1, max = 42.6). We limited the selection to landscapes that were crossed by a power line corridor of at least 1 km in length when selecting those that required the presence of a power line corridor. The area of semi-natural pastures of high nature value in the landscape was calculated using the Swedish National Survey of semi-natural pastures and meadows (TUVA: http://www.jordbruksverket.se/tuva).

In each of the 32 landscapes we selected five grassland habitats: one grazed (or recently grazed) semi-natural grassland of high nature value, one road verge along a large paved road, one road verge along a small gravel road, one uncultivated field border and, in landscapes where present, one power line corridor. The average distance between landscape centroids was 82.1 km (min = 2.82 km, max = 190.8 km). The minimum average distance between habitat types within a landscape was 218.5 m while the maximum average was 1551.5 m. The average distance between the centroid of each transect and the closest edge of the landscape was 322.4 m (min = 2.5 m, max = 933 m). Power line corridors in Sweden are typically maintained by clearing young trees and shrubs in 8-year cycles. Among the selected power line corridors, the earliest succession was in a corridor mowed the same year of the surveys, while the oldest succession occurred in a corridor mowed 6 years before. The average time since the last mowing for all 16 power line corridors was approximately 3 years (Table S2).

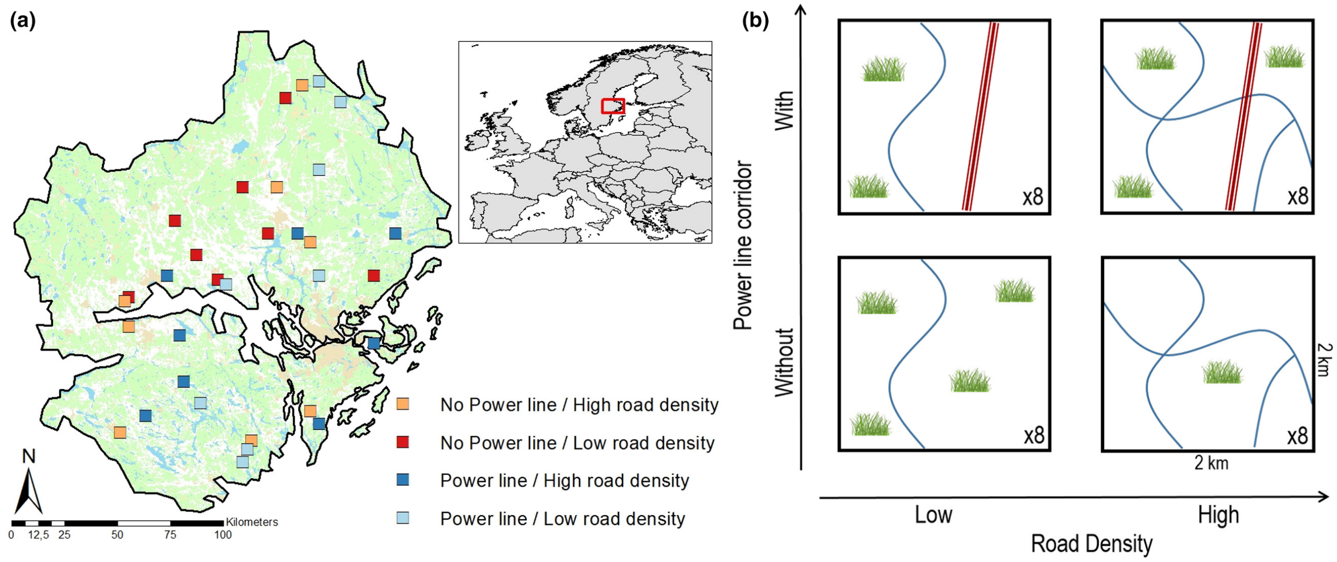

FIGURE 1 (a) Location of the 32 landscapes and (b) study design. Each one of the 32 4 km^2 landscapes belongs to one of four categories, in which the amount of linear infrastructure habitats and semi-natural pastures (illustrated by grass tufts) was different.

2.2 | Plant and flower-visiting insect surveys

In 2016, we surveyed plants, bumblebees and butterflies in the five types of grassland habitat in each of the 32 landscapes. In each of the selected habitats, we established a 200 m long transect (site), which was divided into four 50 m sections. For the plant survey, we placed a 1 m^2 quadratic sample plot in the middle of each section. All plant species belonging to a predefined list of 169 species that are frequently occurring in various types of grassland habitat were recorded (Table S3). Therefore, each plant species could have a maximum of four occurrences per transect (one for each plot). The list contained the absolute majority of the species present across all sites. Plants were surveyed once per site, between the 13 July and the 24 August 2016, at each site.

Butterflies and burnet moths were surveyed along the transect by counting the number of individuals of each species observed within five metres (5 m in front and upwards and 2.5 m to each side) in each direction from the observer. The observer walked the transect at a slow pace, approximately 10 min effective walking time for the 200 m transect. The time was stopped when handling butterflies and for taking notes. When performing the survey in road verges narrower than 5 m, all individuals in the road verge were noted. Because burnet moths (Zygaenidae, with five species occurring in the study region) are diurnal and have similar requirements to day-flying butterflies, they were also included among 'butterflies'. The two cryptic butterfly species *Leptidea sinapis* and *L. juvernica* are virtually impossible to distinguish in the field (Dincă et al., 2011), and were pooled. Butterfly species that could not be visually identified were caught with a net and identified using a Swedish field guide (Söderström, 2006). Bumblebees were surveyed along the same transect, but with a 1 m width. All individuals were caught with a net and identified using a Swedish field guide (Söderström, 2013). Bumblebees that could not be identified in the field were collected and then identified in the laboratory. However, no bumblebee queens were collected to minimize impacts on the sampled populations. Butterflies and bumblebees were surveyed four times at each transect between 1 June and 23 August 2016, between 10:00 and 16:00 h, on days without precipitation, and when the temperature was above 17°C if the weather was sunny or above 20°C if the weather was cloudy. The sequence of sites visited on the same day was randomized to minimize any bias due to the diel activity pattern of the insects. To avoid collector bias, the surveyors ($n = 6$) examined all habitats at least once. This study did not require an ethical approval.

2.3 | Statistical analyses

All statistics were performed using the R software (R Core Team, 2020). We tested for differences in α-diversity among grassland habitats for plants ($n = 132$), butterflies ($n = 133$) and bumblebees ($n = 133$) separately by performing generalized linear mixed models (GLMM) with a Poisson distribution and a log link with species richness of each species group as response variables (package 'LME4', Bates et al., 2015). We included the local type of habitat (factor: five types of grassland habitat), area of semi-natural pastures in the landscape (continuous), the presence or absence of power line corridors in the landscape (factor: present or absent) and the density of the road verges in the landscape (factor: high or low) as fixed explanatory variables. A random intercept for landscape identity was added to account for the nested nature of the design. We tested the interactions between all variables using separate models (Table S6). Each possible two-way interaction was added at a time to the base model (with main effects only) and the resulting AICc values were used for model selection. If the ΔAICc was less than two, the simplest model was chosen. To further explore differences in species richness among habitats, we performed a post-hoc test using the EMMEANS package (Lenth, 2020). We verified that our statistical models exhibited no evidence of spatial autocorrelation by computing spline correlograms of the models' residuals (with bootstrap confidence intervals based on 1000 resamples), using the centroid of transects as estimates of the geographical coordinates of sampling sites (Figure S2).

To assess β-diversity among habitat types, we first performed a nonmetric multidimensional scaling (NMDS) ordination analysis using the VEGAN package (Oksanen et al., 2020) to visualize differences in the community composition among habitat types for each species group. Then, we performed a clustering analysis based on pairwise abundance-based Bray–Curtis dissimilarity distances to explore which habitats had dissimilar community compositions. As for the analyses of species richness, we tested that our inferences based on β-diversity did not suffer from spatial autocorrelation. For this purpose, we computed spline correlograms based here, for each taxon, on the Bray–Curtis distance between species' assemblages and the centroid of transects. Again, we found no evidence of spatial autocorrelation at any distance (Figure S3), showing that community composition was not geographically autocorrelated in our study.

To determine if the dissimilarities in community composition among habitat types were statistically significant and whether they were affected by the amount of habitat in the landscape, we first performed a permutational analysis of variance (PERMANOVA, *adonis2* function in 'VEGAN'). For this analysis, we used the same explanatory variables as above but since the model used Type I sum of squares, the order of the fixed effects was important. We included the variables in the following order: type of habitat (factor: five types of grassland habitat), power line corridors (factor: present or absent), road verge density (factor: high or low) and area of semi-natural pastures in the landscape (continuous). The order was based on our main questions: (1) we explored the dissimilarities in the community composition *among* habitat types, (2) whether these differences depended on the amount of linear infrastructure habitats in the landscape and (3) the effect of area land cover of semi-natural pastures in the landscape. Additionally, we included the landscape identity as the nesting variable to account for several habitats having been sampled in each landscape.

Subsequently, we ran a series of *pairwise* PERMANOVA analyses using the same explanatory variables as above to determine whether the community composition of each species group statistically differed *between* pairs of habitat types. We used the Holm method to correct for the mass-significance that can arise when performing multiple comparisons. This method rejects hypotheses sequentially until no further rejections can be done and adjusts the p values according to the number of tested hypotheses (Holm, 1979). For this analysis, we also tested the interactions between the explanatory variables and chose the simplest model when the ΔAICc was less than two.

To further explore the variation in community composition we calculated total β-diversity, as well as the nestedness and turnover components, for each organism group in each habitat, using the R package BETAPART (Baselga & Orme, 2012). Total β-diversity was measured as the Sørensen-based *multiple-site* dissimilarity (β_{SOR}, incidence based), and the value of the turnover component was measured as Simpson-based multiple-site dissimilarity (β_{SIM}). The nestedness component (β_{NES}) is then measured as the nestedness-resultant fraction of the Sørensen dissimilarity function (Baselga, 2010; 'beta.multi' with 'Sorensen' as the index family in the BETAPART package). *Pairwise* β-diversity (β_{sor}, incidence-based *pairwise* dissimilarities), together with the turnover component (β_{sim}) and the nestedness-resultant component (β_{nes}), were calculated between each pair of habitat type using the function 'beta. pair' in the package BETAPART.

Finally, we used the package INDICSPECIES (Cáceres & Legendre, 2009) to identify species ('indicator species') that have strong associations to certain habitat types (i.e. species that occur more frequently in one habitat type, compared to the other habitat types, than expected by random). This package uses an extension of the *Indicator value* (IndVal; Dufrêne & Legendre, 1997) to measure the association between a species and a site, and a combination of sites. The package uses a permutation test to determine the significance of the association, which is based on the abundance and persistence of the species occurrence in each habitat.

3 | RESULTS

We recorded a total of 133 plant species, 4240 butterfly individuals belonging to 53 species, and 1785 bumblebee individuals belonging to 19 species (Table S4). Species accumulation curves indicate that most of the surveys resulted in a good representation of the fauna and flora in the individual grassland habitats (Figures S4–S6).

3.1 | Alpha diversity

Species richness of butterflies and plants, but not of bumblebees, differed among habitat types (Figure 2). For butterflies, α-diversity was highest in power line corridors and semi-natural pastures, and there was no difference in α-diversity between pastures and road verges of small roads (Figure 2). The α-diversity of plants was as high in power line corridors and road verges as in semi-natural pastures. Road verges along big roads had lower α-diversity of plants than verges along small roads, and the lowest α-diversity was found in uncultivated field borders (Figure 2). Furthermore, plant α-diversity, irrespective of habitat type, was higher in landscapes with than in landscapes without a power line corridor (Table 1). For bumblebees, the null model had the lowest AICc value, meaning that the landscape variables did not influence α-diversity (Tables S5 and S6). For plants and butterflies, some models with interactions performed equally well (ΔAICc <2) as the model without interactions, but none

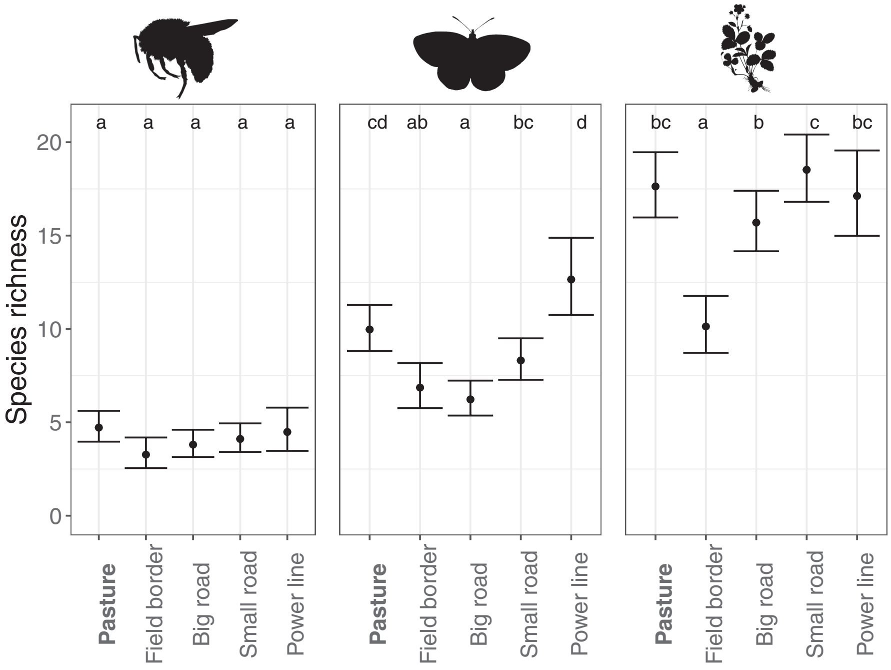

FIGURE 2 Differences in species richness per habitat for bumblebees, butterflies and plants (from left to right). The figures show the results of the GLMM exploring the influence of the amount of linear infrastructure habitats and semi-natural pastures in the landscape. The letters above each habitat type are the results from the post-hoc analyses: habitats that do not share a letter are significantly different from each other.

TABLE 1 Results from the generalized linear mixed model exploring differences in species richness of each species group per site, and how they are affected by the amount of habitat in the landscape. Shown are the Chi-square values (χ^2), degrees of freedom (d.f.) and *p*-values (*p*). *p*-values in bold are significant at the 0.05 level.

Response variable	Predictor	χ^2	df	*p*
Butterfly species richness	Habitat type*	61.08	4	**<0.001**
	SNG	1.17	1	0.28
	PL	0.08	1	0.78
	RD	3.53	1	0.06
Plant species richness	Habitat type*	59.51	4	**<0.001**
	SNG	0.83	1	0.36
	PL	6.09	1	**0.01**
	RD	0.00	1	1.00

Abbreviations: PL, the presence/absence of power line corridors in the landscape; SNG, area of semi-natural pastures in the landscape; RD, road verge density in the landscape (high/low).

*The estimates, standard errors, *z*-values and *p*-values for individual habitat types are found in Table S5.

of the interactions between habitat type and the landscape parameters were statistically significant.

3.2 | Beta diversity

The NMDS analysis showed relatively large overlaps in community composition among the five habitat types, especially for bumblebees and butterflies (Figure 3a; Figures S7–S9). In combination with the clustering analysis (Figure 3b), the NMDS showed that plant communities in field borders and power line corridors were relatively distinct from that in semi-natural pastures and road verges, which had large overlaps in composition. For butterflies, the community composition in power line corridors was the most distinct compared to all other habitat types, and for bumblebees, the same was the case for field borders (Figure 3). The patterns from the NMDS were confirmed by the PERMANOVA (Table 2) and pairwise PERMANOVA analyses (Table S7), which showed differences in community composition among habitat types for all taxa. The PERMANOVA analysis also showed that road verge density and the area of semi-natural pastures in the landscape, but not the presence of power line corridors, influenced the overall community composition of butterflies and plants. However, neither road verge density or the area of semi-natural pastures in the landscape interacted with habitat type (Table S8), indicating that even though the area of road verges and semi-natural pastures in the landscape influenced local community composition, they did not affect the similarity of communities among the grassland types. As for α-diversity, the lowest AICc for the bumblebees was for the null model, indicating that the landscape variables had no influence on the species composition (Table S8).

β-diversity of butterflies and plants among habitat types was driven to a greater extent by species turnover than by nestedness (Figure 4; butterflies: $\beta_{SOR} = 0.390$, $\beta_{SIM} = 0.234$, $\beta_{NES} = 0.157$; plants: $\beta_{SOR} = 0.465$, $\beta_{SIM} = 0.295$, $\beta_{NES} = 0.170$). In other words, differences in the community composition between habitats for these two groups were mainly due to the replacement of species among habitat types (Figure S10). In contrast, the β-diversity of bumblebee communities was to a larger extent due to nestedness, meaning that the communities in sites with fewer species were a subset of the communities with a higher number of species ($\beta_{SOR} = 0.132$, $\beta_{SIM} = 0.057$, $\beta_{NES} = 0.074$).

The indicator species analyses identified 71 species that were more likely to occur in specific habitats than others (Table S9). Seven plant species, one bumblebee species (*B. ruderarius*), but no butterfly species, were associated with semi-natural pastures. Nine butterfly species and 18 plant species were more likely to occur in power line corridors. Road verges had the least number of indicator species of all groups with only two plant species more likely to occur in each type of verge. There were no insect indicator species in field borders, but seven plant species were most likely to occur in this habitat type.

4 | DISCUSSION

We explored to what extent linear infrastructure habitats can support plant and insect species linked to traditionally managed semi-natural pastures. Power line corridors and road verges contained similar numbers of plant and insect species as traditionally managed semi-natural pastures of high nature value. In addition, we found that power line corridors enrich landscapes with plant species. However, the community composition of plants, butterflies and bumblebees (only in road verges along small roads) in linear infrastructure habitats differed from that in semi-natural pastures, showing that they support a subset of the species found in semi-natural pastures.

The α-diversity of plants and bumblebees in road verges and power line corridors was similar to the α-diversity in semi-natural pastures of high nature value as we predicted. This is in line with previous findings that road verges can have high numbers of plant, butterfly and bumblebee species (Auffret & Lindgren, 2020; Saarinen et al., 2005) and that the species richness of these groups in power line corridors can be comparable to that in semi-natural pastures (Berg et al., 2016; Hill & Bartomeus, 2016; Russell et al., 2005). Hence, we confirm that novel grassland habitats along linear infrastructure can support a large number of grassland species.

Previously, we found that the ϒ-diversity of plants was higher in landscapes with power line corridors, possibly because the power line corridors add grassland habitat to the landscape (Dániel-Ferreira et al., 2020). Here, we found that power line corridors in the landscape also had a positive effect on plant α-diversity in each grassland type, but there was no such effect for either of the insect groups. We suspect that the contribution of power line corridors to landscape-scale biodiversity will be more important

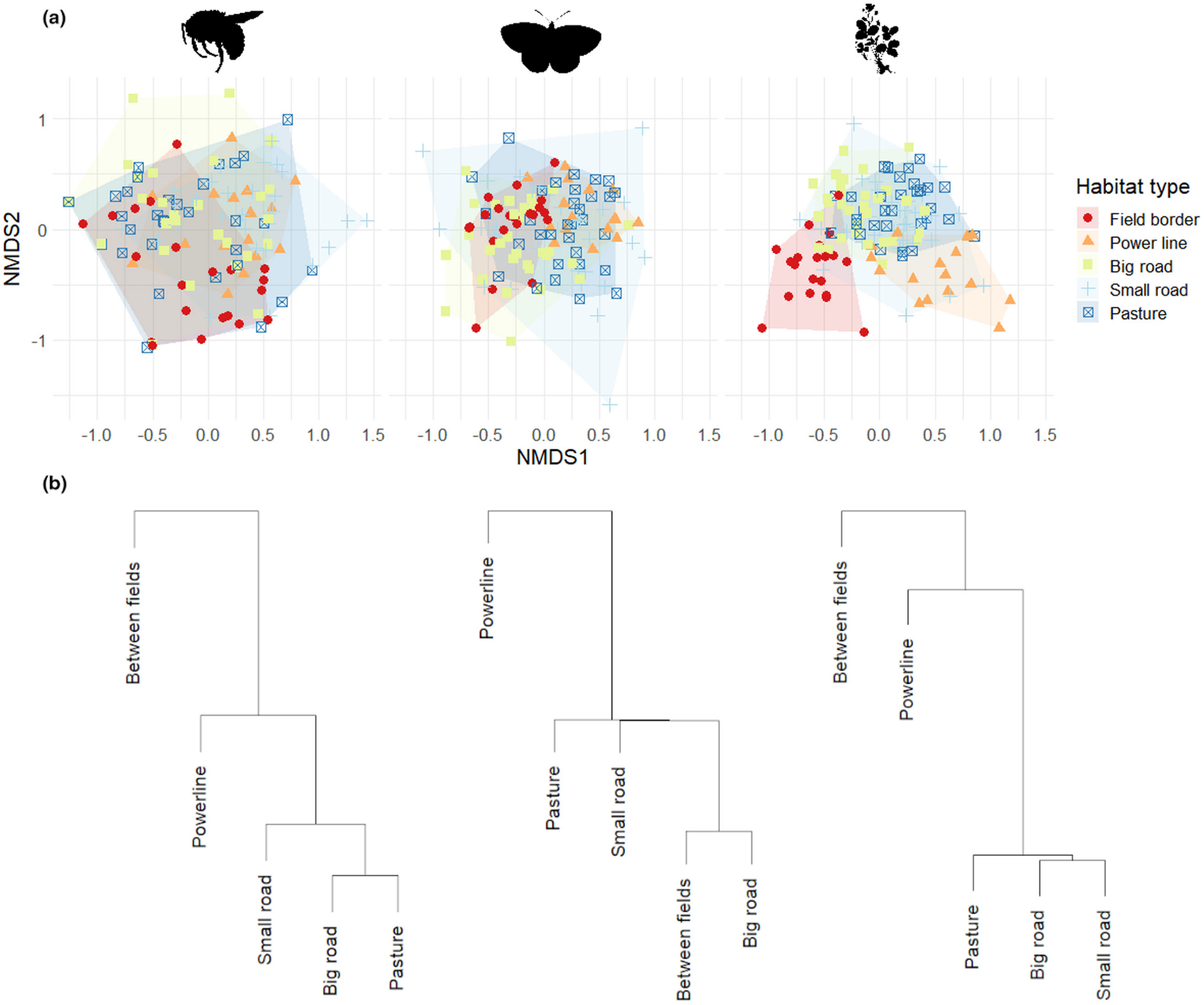

FIGURE 3 (a) Nonmetric multidimensional scaling (NMDS) analyses for bumblebees (stress = 0.17), butterflies (stress = 0.20) and plants (stress = 0.19) (from left to right) in the five types of grassland habitats. (b) Clustering analysis based on Bray–Curtis distances. The figure shows differences and similarities in community composition among habitat types for bumblebees, butterflies and plants (from left to right). Habitat types that are clustered together have a more similar community composition.

in landscapes where very few other grassland habitat remain. The species richness of butterflies in all habitat types tended to decrease in landscapes with a high density of road verges, and hence roads. This result might be due to an interaction between local and landscape factors. For instance, Miljanic et al. (2019) found that the diversity of bees in forest patches in the United States responded to an interaction between local management and landscape composition and configuration. This could be the case for this study as well, such that the management applied to the road verges and other local factors exclusive only to the road verges (e.g. pollution, turbulence and noise) can be interacting with the landscape context. Interestingly, Kallioniemi et al. (2017) found a similar negative effect of road density on bumblebee species richness and density, possibly attributed to traffic mortality or road verge management.

Contrary to our expectations and previous observations (Janišová et al., 2014; Öckinger & Smith, 2006), the area of semi-natural grasslands of high nature value in the landscape did not affect the α-diversity of plants or butterflies. The lack of such an effect could depend on the spatial scale on which habitat amount was measured, or on the distance to the closest semi-natural grassland patch (Bergman et al., 2018; Öckinger & Smith, 2007b).

As predicted, there was a high degree of overlap in community composition among habitat types for all species groups. Similarities in the composition of species between linear infrastructure habitats and managed grasslands have also been documented for plants, insects, amphibians, reptiles, mammals and birds (Gardiner et al., 2018). However, the pairwise PERMANOVA showed differences in the community composition of plants and insects between pairs of habitat types. This, in combination with the fact that β-diversity of plants

TABLE 2 Results from the PERMANOVA analysis of dissimilarities in community composition among sites and how the amount of grassland habitat in the landscape affects them. Results are based on abundances and Bray–Curtis dissimilarities. The model included the landscape identity as a random component to the model. Shown are the degrees of freedom (df), sums of squares (SS), *F*-statistics (*F*), coefficients of partial determination (R^2), and *p*-values (*p*). Values were obtained using 999 permutations. The terms were added sequentially to the model in the following order: habitat type, power line corridor (PL), road verge density in the landscape (RD) and area of semi-natural pastures (SNG). *p*-values in bold are significant at the 0.05 level.

Taxon	Source	df	SS	*F*	R^2	*p*
Butterflies	Habitat type	4	3.30	3.70	0.10	**<0.001**
	PL	1	0.25	1.14	0.01	0.85
	RD	1	0.31	1.40	0.01	**<0.001**
	SNG	1	0.26	1.16	0.01	**<0.001**
	Residual	125	27.81		0.87	
	Total	132	31.93		1	
Plants	Habitat type	4	6.74	6.84	0.18	**<0.001**
	PL	1	0.31	1.25	0.01	1.00
	RD	1	0.32	1.29	0.01	**<0.001**
	SNG	1	0.54	2.18	0.01	**<0.001**
	Residual	124	30.58		0.79	
	Total	131	38.49		1	

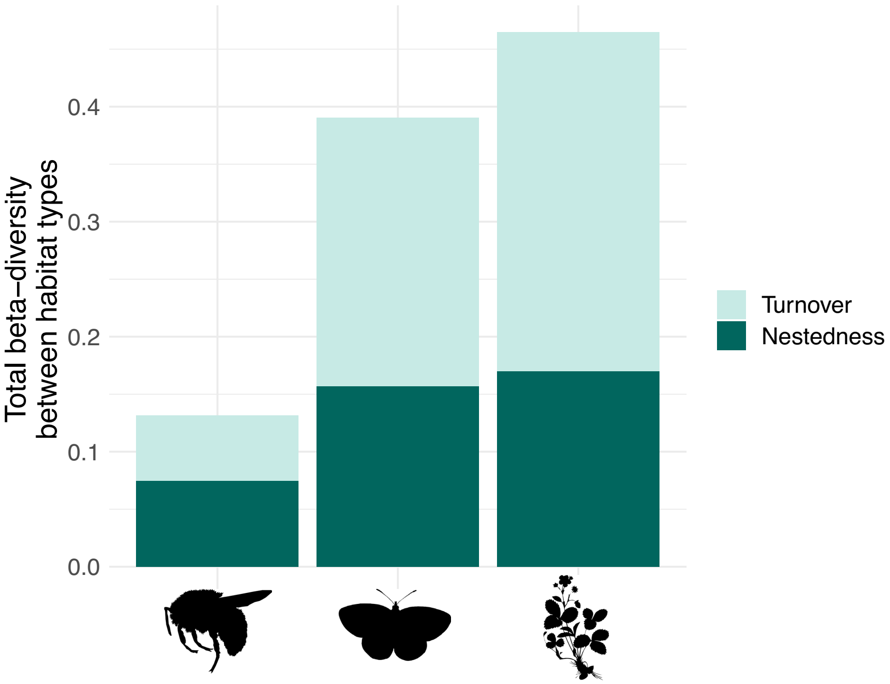

FIGURE 4 Total beta diversity (β_{SOR}) between habitat types for all species groups (from left to right: bumblebees, butterflies and plants) partitioned into the turnover (β_{SIM}) and nestedness (β_{NES}) components.

and butterflies was mainly driven by species turnover among habitat types, suggests that despite the similarities in α- and β-diversity between habitat types, linear infrastructure habitats are not able to fully replace semi-natural pastures of high nature value.

We found no support for our prediction of a lower β-diversity in landscapes with a high amount of grassland habitats. While the areas of semi-natural grasslands and road verges in the landscape influenced the overall composition of plant and butterfly communities, the areas of these habitats in the landscape did not influence the (dis)similarity of communities in different habitats in the same landscape. Apparently, a large grassland area in the landscape did not increase dispersal among habitats to the extent that communities became homogenized. One reason for this could be that the structural connectivity, such as a high density of linear infrastructure habitats, is a poor predictor of species realized dispersal through the landscape (e.g. functional connectivity) (Baguette et al., 2013). For instance, Kimberley et al. (2021) showed that generalist plant species responded negatively to structural connectivity, while the occurrence of specialist species was mostly determined by functional connectivity. Therefore, the β-diversity patterns observed in this study might be due to the contrasting responses of generalists and specialists to landscape connectivity.

The total β-diversity of bumblebees was relatively low and, in contrast to plants and butterflies, it was mostly driven by nestedness, that is, species-poor communities were a subset of the richer communities. Indeed, most bumblebee species were observed in all grassland habitats, except for a couple of species that did not occur in all habitats. *B. jonellus* was only observed in pastures (*n* = 2) while *B. distinguendus* (NT) was not recorded in pastures, verges of small roads or power lines. This was not surprising, given that all bumblebees have broad dietary niches and the ability to fly long distances in search for food (Osborne et al., 2008). Hence, a snapshot pattern of their distribution, as in our study, might not show the full picture of the importance of different habitat types for bumblebee population persistence (Iles et al., 2018). Further studies on the spatial distribution of nest sites for different bumblebee species, and on the temporal variability of flower resources over the season in the different habitat types could shed more light on the importance of grasslands along linear infrastructure for bumblebees.

The differences in community composition among habitat types could be explained by soil conditions, management, and influences from the surrounding land. Plant communities in road verges tend to have a high degree of generalists, as well as a low proportion of species that grow in nutrient poor soils (Cousins, 2006; Hooftman et al., 2021; Vanneste et al., 2020). We found that the plants *Cirsium arvense*, *Elymus repens* and *Urtica dioica*, which all grow on nitrogen-rich soils were typical for uncultivated field borders, as indicated by the indicator species analysis. This could be explained by nutrient run-off from adjacent agricultural fields (Lundkvist & Fogelfors, 2004). Power lines also had relatively distinct plant communities, with woody species like *Betula pendula* and *Rubus idaeus*, and forest plants like *Vaccinium vitis-idaea* and *Convallaria majalis*. This partly reflects the neighbouring forest habitat, which could influence communities in power line corridors by immigration of forest species but also through differences in sun exposure and temperature due to shading from the forest, or their much lower-intensity management compared to the other grassland types (Steinert et al., 2018). Interestingly, all plant species that were strongly associated with semi-natural pastures are dependent on continuously managed grasslands (Ekstam & Forshed, 1992), indicating that the most specialized grassland species are rarely found in the novel grasslands.

The β-diversity of butterflies was mostly driven by turnover among habitat types. This could partly be explained by the high degree of specialization of many butterflies in their larval stage, resulting in close associations between grassland plant and butterfly communities (Dainese et al., 2017). In addition, butterfly community composition is often related to vegetation structure (Berg et al., 2013). Especially the power line corridors, which typically have a high cover of woody plants, had a distinct butterfly community composition. This was also reflected in the indicator species analysis where species feeding on common forest dwarf shrubs, such as *Plebejus argus* and *P. idas* feeding on *Calluna vulgaris* and *P. optilete* feeding on *Vaccinium vitis-idaea*, were identified as typical for power line corridors.

4.1 | Implications for grassland biodiversity

We demonstrated that road verges and power line corridors can have as high α-diversity of plants, butterflies and bumblebees as semi-natural pastures of high nature value and are important for biodiversity conservation. Despite large similarities in community composition among habitat types, the composition of plant and butterfly communities especially in power line corridors and field borders differed from that in semi-natural pastures. Especially the most specialized grassland species were typically lacking from the infrastructure habitats. This shows that although valuable, infrastructure habitats are no substitute for core semi-natural grassland habitat. Therefore, protecting and restoring semi-natural grasslands should continue to be a priority for the conservation of grassland biodiversity.

However, the large similarity in the community composition of all species groups among habitat types indicates that linear infrastructure habitats, especially road verges, can be important for maintaining viable population sizes of these species by increasing their habitat area. Our results indicate that linear infrastructure habitats are particularly important for species that are 'intermediately common', that is, not the most specialized species, which might only occur in semi-natural pastures, nor the most generalist species.

Infrastructure habitats in landscapes with small amounts of semi-natural pastures did not have reduced α-diversity of plants and butterflies compared with landscapes with large areas of semi-natural pastures. This shows that in landscapes where few or no semi-natural pastures remain, a considerable proportion of the grassland biodiversity is found in the infrastructure habitats. In these landscapes, many grassland species will benefit from biodiversity-targeted management of linear infrastructure habitats.

AUTHOR CONTRIBUTIONS

Juliana Dániel-Ferreira was involved in data curation, formal analysis, writing—original draft and visualization. Yoan Fourcade was involved in data curation, formal analysis, visualization and writing—review and editing. Riccardo Bommarco was involved in conceptualization and writing—review and editing. Jörgen Wissman was involved in conceptualization, methodology and writing—review and editing. Erik Öckinger was involved in conceptualization, methodology, resources, writing—review and editing, supervision, project administration and funding acquisition.

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CONFLICT OF INTEREST STATEMENT

Erik Öckinger is an Editor of Journal of Applied Ecology, but took no part in the peer review and decision-making processes for this paper. The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from FigShare https://doi.org/10.6084/m9.figshare.22178651.v1 (Dániel-Ferreira et al., 2023).

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REFERENCES

Auffret, A. G., & Lindgren, E. (2020). Roadside diversity in relation to age and surrounding source habitat: Evidence for long time lags in valuable green infrastructure. *Ecological Solutions and Evidence*, *1*(1), e12005. https://doi.org/10.1002/2688-8319.12005

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, *88*(2), 310–326. https://doi.org/10.1111/brv.12000

Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*(1), 134–143. https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A., & Orme, C. D. L. (2012). Betapart: An R package for the study of beta diversity: *Betapart package*. *Methods in Ecology and Evolution*, *3*(5), 808–812. https://doi.org/10.1111/j.2041-210X.2012.00224.x

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*(1), 1–48. https://doi.org/10.18637/jss.v067.i01

Bengtsson, J., Bullock, J. M., Egoh, B., Everson, C., Everson, T., O'Connor, T., O'Farrell, P. J., Smith, H. G., & Lindborg, R. (2019). Grasslands—More important for ecosystem services than you might think. *Ecosphere*, *10*(2), e02582. https://doi.org/10.1002/ecs2.2582

Berg, Å., Ahrné, K., Öckinger, E., Svensson, R., & Söderström, B. (2011). Butterfly distribution and abundance is affected by variation in the Swedish forest-farmland landscape. *Biological Conservation*, *144*(12), 2819–2831. https://doi.org/10.1016/j.biocon.2011.07.035

Berg, Å., Ahrné, K., Öckinger, E., Svensson, R., & Wissman, J. (2013). Butterflies in semi-natural pastures and power-line corridors—Effects of flower richness, management, and structural vegetation characteristics. *Insect Conservation and Diversity*, *6*(6), 639–657. https://doi.org/10.1111/icad.12019

Berg, Å., Bergman, K.-O., Wissman, J., Żmihorski, M., & Öckinger, E. (2016). Power-line corridors as source habitat for butterflies in forest landscapes. *Biological Conservation*, *201*, 320–326. https://doi.org/10.1016/j.biocon.2016.07.034

Bergman, K.-O., Burman, J., Jonason, D., Larsson, M. C., Ryrholm, N., Westerberg, L., & Milberg, P. (2020). Clear-cuts are temporary habitats, not matrix, for endangered grassland burnet moths (*Zygaena* spp.). *Journal of Insect Conservation*, *24*(2), 269–277. https://doi.org/10.1007/s10841-019-00193-3

Bergman, K.-O., Dániel-Ferreira, J., Milberg, P., Öckinger, E., & Westerberg, L. (2018). Butterflies in Swedish grasslands benefit from forest and respond to landscape composition at different spatial scales. *Landscape Ecology*, *33*(12), 2189–2204. https://doi.org/10.1007/s10980-018-0732-y

Cáceres, M. D., & Legendre, P. (2009). Associations between species and groups of sites: Indices and statistical inference. *Ecology*, *90*(12), 3566–3574. https://doi.org/10.1890/08-1823.1

Cousins, S. A. O. (2006). Plant species richness in midfield islets and road verges—The effect of landscape fragmentation. *Biological Conservation*, *127*(4), 500–509. https://doi.org/10.1016/j.biocon.2005.09.009

Cousins, S. A. O., Auffret, A. G., Lindgren, J., & Tränk, L. (2015). Regional-scale land-cover change during the 20th century and its consequences for biodiversity. *Ambio*, *44*(S1), 17–27. https://doi.org/10.1007/s13280-014-0585-9

Dainese, M., Isaac, N. J. B., Powney, G. D., Bommarco, R., Öckinger, E., Kuussaari, M., Pöyry, J., Benton, T. G., Gabriel, D., Hodgson, J. A., Kunin, W. E., Lindborg, R., Sait, S. M., & Marini, L. (2017). Landscape simplification weakens the association between terrestrial producer and consumer diversity in Europe. *Global Change Biology*, *23*(8), 3040–3051. https://doi.org/10.1111/gcb.13601

Dániel-Ferreira, J., Bommarco, R., Wissman, J., & Öckinger, E. (2020). Linear infrastructure habitats increase landscape-scale diversity of plants but not of flower-visiting insects. *Scientific Reports*, *10*(1), 21374. https://doi.org/10.1038/s41598-020-78090-y

Dániel-Ferreira, J., Fourcade, Y., Bommarco, R., Wissman, J., & Öckinger, E. (2023). Data from: Communities in infrastructure habitats are species-rich but only partly support species associated with semi-natural grasslands. *Figshare*, https://doi.org/10.6084/m9.figshare.22178651.v1

Dincă, V., Lukhtanov, V. A., Talavera, G., & Vila, R. (2011). Unexpected layers of cryptic diversity in wood white Leptidea butterflies. *Nature Communications*, *2*(1), 324. https://doi.org/10.1038/ncomms1329

Dormann, C. F., Schweiger, O., Augenstein, I., Bailey, D., Billeter, R., Blust, G. D., DeFilippi, R., Frenzel, M., Hendrickx, F., Herzog, F., Klotz, S., Liira, J., Maelfait, J.-P., Schmidt, T., Speelmans, M., Wingerden, W. K. R. E. V., & Zobel, M. (2007). Effects of landscape structure and land-use intensity on similarity of plant and animal communities. *Global Ecology and Biogeography*, *16*(6), 774–787. https://doi.org/10.1111/j.1466-8238.2007.00344.x

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecological Monographs*, *67*(3), 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Ekstam, U., & Forshed, N. (1992). *Om hävden upphör: Kärlväxter som indikatorarter i ängs- och hagmarker = If grassland management ceases: vascular plants as indicator species in meadows and pastures*. Stat naturvårdsverk.

Feranec, J., Jaffrain, G., Soukup, T., & Hazeu, G. (2010). Determining changes and flows in European landscapes 1990–2000 using CORINE land cover data. *Applied Geography*, *30*(1), 19–35. https://doi.org/10.1016/j.apgeog.2009.07.003

Gardiner, M. M., Riley, C. B., Bommarco, R., & Öckinger, E. (2018). Rights-of-way: A potential conservation resource. *Frontiers in Ecology and the Environment*, *16*(3), 149–158. https://doi.org/10.1002/fee.1778

Gómez-Rodríguez, C., Freijeiro, A., & Baselga, A. (2015). Dispersal and ecological traits explain differences in beta diversity patterns of European beetles. *Journal of Biogeography*, *42*(8), 1526–1537. https://doi.org/10.1111/jbi.12523

Hill, B., & Bartomeus, I. (2016). The potential of electricity transmission corridors in forested areas as bumblebee habitat. *Royal Society Open Science*, *3*(11), 160525. https://doi.org/10.1098/rsos.160525

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, *6*(2), 65–70.

Hooftman, D., Kimberley, A., Cousins, S. A. O., Escribano-Avila, G., Honnay, O., Krickl, P., Plue, J., Poschlod, P., Traveset, A., & Bullock, J. M. (2021). Dispersal limitation, eutrophication and propagule pressure constrain the conservation value of grassland green infrastructure. *Biological Conservation*, *258*, 109152. https://doi.org/10.1016/j.biocon.2021.109152

Iles, D. T., Williams, N. M., & Crone, E. E. (2018). Source-sink dynamics of bumblebees in rapidly changing landscapes. *Journal of Applied Ecology*, *55*(6), 2802–2811. https://doi.org/10.1111/1365-2664.13175

Janišová, M., Michalcová, D., Bacaro, G., & Ghisla, A. (2014). Landscape effects on diversity of semi-natural grasslands. *Agriculture, Ecosystems & Environment*, *182*, 47–58. https://doi.org/10.1016/j.agee.2013.05.022

Jeusset, A., Vargac, M., Bertheau, Y., Coulon, A., Deniaud, N., Flamerie De Lachapelle, F., Jaslier, E., Livoreil, B., Roy, V., Touroult, J., Vanpeene, S., Witté, I., & Sordello, R. (2016). Can linear transportation infrastructure verges constitute a habitat and/or a corridor for biodiversity in temperate landscapes? A systematic review protocol. *Environmental Evidence*, *5*(1), 1–11.

Kallioniemi, E., Åström, J., Rusch, G. M., Dahle, S., Åström, S., & Gjershaug, J. O. (2017). Local resources, linear elements and mass-flowering crops determine bumblebee occurrences in moderately intensified farmlands. *Agriculture, Ecosystems & Environment*, *239*, 90–100. https://doi.org/10.1016/j.agee.2016.12.039

Kimberley, A., Hooftman, D., Bullock, J. M., Honnay, O., Krickl, P., Lindgren, J., Plue, J., Poschlod, P., Traveset, A., & Cousins, S. A. O. (2021). Functional rather than structural connectivity explains grassland plant diversity patterns following landscape scale habitat loss. *Landscape Ecology*, *36*(1), 265–280. https://doi.org/10.1007/s10980-020-01138-x

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., Öckinger, E., Pärtel, M., Pino, J., Rodà, F., Stefanescu, C., Teder, T., Zobel, M., & Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology & Evolution*, *24*(10), 564–571. https://doi.org/10.1016/j.tree.2009.04.011

Lenth, R. (2020). *Emmeans: Estimated marginal means, aka least-squares means*. R Package Version 1.5.2-1. https://CRAN.R-project.org/package=emmeans

Lundkvist, A., & Fogelfors, H. (2004). *Ogräsreglering på åkermark*. Inst. för ekologi och växtproduktionslära, Sveriges lantbruksuniv.

Miljanic, A. S., Loy, X., Gruenewald, D. L., Dobbs, E. K., Gottlieb, I. G., Fletcher, R. J., & Brosi, B. J. (2019). Bee communities in forestry production landscapes: Interactive effects of local-level management and landscape context. *Landscape Ecology*, *34*(5), 1015–1032.

Nielsen, T. F., Sand-Jensen, K., Dornelas, M., & Bruun, H. H. (2019). More is less: Net gain in species richness, but biotic homogenization over 140 years. *Ecology Letters*, *22*(10), 1650–1657. https://doi.org/10.1111/ele.13361

Öckinger, E., Lindborg, R., Sjödin, N. E., & Bommarco, R. (2012). Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, *35*(3), 259–267. https://doi.org/10.1111/j.1600-0587.2011.06870.x

Öckinger, E., & Smith, H. G. (2006). Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia*, *149*(3), 526–534. https://doi.org/10.1007/s00442-006-0464-6

Öckinger, E., & Smith, H. G. (2007a). Asymmetric dispersal and survival indicate population sources for grassland butterflies in agricultural landscapes. *Ecography*, *30*(2), 288–298. https://doi.org/10.1111/j.0906-7590.2007.05048.x

Öckinger, E., & Smith, H. G. (2007b). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology*, *44*(1), 50–59. https://doi.org/10.1111/j.1365-2664.2006.01250.x

Oksanen, J., Blanchet, G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2020). *Vegan: Community ecology package*. R Package Version 2.5-7.

Oldén, A., & Halme, P. (2016). Grazers increase β-diversity of vascular plants and bryophytes in wood-pastures. *Journal of Vegetation Science*, *27*(6), 1084–1093. https://doi.org/10.1111/jvs.12436

Osborne, J. L., Martin, A. P., Carreck, N. L., Swain, J. L., Knight, M. E., Goulson, D., Hale, R. J., & Sanderson, R. A. (2008). Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology*, *77*(2), 406–415. https://doi.org/10.1111/j.1365-2656.2007.01333.x

Phillips, B. B., Gaston, K. J., Bullock, J. M., & Osborne, J. L. (2019). Road verges support pollinators in agricultural landscapes, but are diminished by heavy traffic and summer cutting. *Journal of Applied Ecology*, *56*(10), 2316–2327. https://doi.org/10.1111/1365-2664.13470

Phillips, B. B., Navaratnam, A., Hooper, J., Bullock, J. M., Osborne, J. L., & Gaston, K. J. (2021). Road verge extent and habitat composition across Great Britain. *Landscape and Urban Planning*, *214*, 104159. https://doi.org/10.1016/j.landurbplan.2021.104159

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Ruhí, A., Datry, T., & Sabo, J. L. (2017). Interpreting beta-diversity components over time to conserve metacommunities in highly dynamic ecosystems. *Conservation Biology*, *31*(6), 1459–1468. https://doi.org/10.1111/cobi.12906

Russell, K. N., Ikerd, H., & Droege, S. (2005). The potential conservation value of unmowed powerline strips for native bees. *Biological Conservation*, *124*(1), 133–148. https://doi.org/10.1016/j.biocon.2005.01.022

Saarinen, K., Valtonen, A., Jantunen, J., & Saarnio, S. (2005). Butterflies and diurnal moths along road verges: Does road type affect diversity and abundance? *Biological Conservation*, *123*(3), 403–412. https://doi.org/10.1016/j.biocon.2004.12.012

Santana, J., Porto, M., Reino, L., Moreira, F., Ribeiro, P. F., Santos, J. L., Rotenberry, J. T., & Beja, P. (2017). Using beta diversity to inform agricultural policies and conservation actions on Mediterranean farmland. *Journal of Applied Ecology*, *54*(6), 1825–1835. https://doi.org/10.1111/1365-2664.12898

Söderström, B. (2006). *Svenska fjärilar: en fälthandbok*. Alberts Bonniers Förlag.

Söderström, B. (2013). *Sveriges humlor—En fälthandbok*. Entomologiska Föreningen i Stockholm.

Steinert, M., Moe, S. R., Sydenham, M. A. K., & Eldegard, K. (2018). Different cutting regimes improve species and functional diversity of insect-pollinated plants in power-line clearings. *Ecosphere*, *9*(11), e02509. https://doi.org/10.1002/ecs2.2509

Strijker, D. (2005). Marginal lands in Europe—Causes of decline. *Basic and Applied Ecology*, *6*(2), 99–106. https://doi.org/10.1016/j.baae.2005.01.001

Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T. O., Dormann, C. F., Ewers, R. M., Fründ, J., Holt, R. D., Holzschuh, A., Klein, A. M., Kleijn, D., Kremen, C., Landis, D. A., Laurance, W., … Westphal, C. (2012). Landscape moderation of biodiversity patterns and processes—Eight hypotheses. *Biological Reviews*, *87*(3), 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x

Vanneste, T., Govaert, S., Kesel, W. D., Berge, S. V. D., Vangansbeke, P., Meeussen, C., Brunet, J., Cousins, S. A. O., Decocq, G., Diekmann, M., Graae, B. J., Hedwall, P.-O., Heinken, T., Helsen, K., Kapás, R. E., Lenoir, J., Liira, J., Lindmo, S., Litza, K., … Frenne, P. D. (2020). Plant diversity in hedgerows and road verges across Europe. *Journal of Applied Ecology*, *57*(7), 1244–1257. https://doi.org/10.1111/1365-2664.13620

Villemey, A., Jeusset, A., Vargac, M., Bertheau, Y., Coulon, A., Touroult, J., Vanpeene, S., Castagneyrol, B., Jactel, H., Witte, I., Deniaud, N., Flamerie De Lachapelle, F., Jaslier, E., Roy, V., Guinard, E., Le Mitouard, E., Rauel, V., & Sordello, R. (2018). Can linear transportation infrastructure verges constitute a habitat and/or a corridor for insects in temperate landscapes? A systematic review. *Environmental Evidence*, *7*(1). https://doi.org/10.1186/s13750-018-0117-3

Whittaker, R. H. (1960). Vegetation of the Siskiyou Mountains, Oregon and California. *Ecological Monographs*, *30*(3), 279–338. https://doi.org/10.2307/1943563

SUPPORTING INFORMATION

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Communities in infrastructure habitats are species-rich but only partly support species associated with semi-natural grasslands

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Supplementary information

Table S1. Summary of the road and road verge characteristics in each landscape category. The road length was measured at the landscape scale (4 km^2) for all landscapes separately. The width of the road verges was measured at the sample sites. Some sites lacked a measurement, and the presented average and standard deviations (± SD) are based only in the measured sites. The n corresponds to the column to the immediate left.

Landscape Category	Average road length in the landscape (km ± SD)	Average width of road verges along big paved roads (m ± SD)	n	Average width of road verges along small gravel roads (m ± SD)	n
No Power line / High road density	14.70 (± 1.28)	2.95 (± 0.86)	8	2.86 (± 0.60)	7
No Power line / Low road density	5.54 (± 1.28)	2.47 (± 0.37)	8	2.92 (± 0.12)	3
Power line / High road density	17.88 (± 6.65)	3.02 (± 1.02)	8	3.13 (± 1.28)	7
Power line/ Low road density	4.45 (± 0.85)	2.96 (± 1.04)	7	2.86 (± 0.78)	7

Table S2. Summary of the characteristics of the power line corridors in each landscape category. The width of the power-line corridors was measured at the sample sites. Some sites lacked a measurement, and the presented average and standard deviations (± SD) are based only in the measured sites.

Landscape Category	Average width power-line corridors (m ± SD)	n	Average years since mown (±SD)
Power line / High road density	41.43 (± 8.00)	7	2.75 (± 1.64)
Power line / Low road density	55.25 (± 15.00)	6	3.00 (± 1.32)

Table S3. Species included the in the pre-defined list used during the plant inventories. The list contains the absolute majority of species that can be found in semi-natural grasslands in Sweden. Note that not all the species listed below were observed in the study.

Acer platanoides
Achillea millefolium
Achillea ptarmica
Agrimona eupatoria
Agrostis capillaris
Agrostis gigantean
Agrostis stolinifera
Ajuga pyramidalis
Alchemilla glabra
Alchemilla glaucescens
Alchemilla monticola
Allium oleraceum
Alnus glutinosa
Alopecurus geniculatus
Alopercurus pratensis
Anemone nemorosa
Antennaria dioica
Anthoxanthum odoratum
Anthriscus sylvestris
Anthyllis vulneraria
Arenaria serpyllifolia
Arrhenatherum pratensis
Arrhenahterum pubescens
Betula pendula
Bistorta vivipara
Briza media
Calluna vulgaris
Campanula persicifolia
Campanula rotundifolia
Cardamine pratensis
Carex caryophyllea
Carex flacca
Carex hirta
Carex nigra
Carex ovalis
Carex pallescens
Carex panacea
Carex spicata
Carlina vulgaris
Carum carvi
Centaurea jacea
Cerastium fontanum
Cirsium arvense
Cirsium palustre
Convallaria majalis
Dactylis glomerata
Dactylorhiza latifolia
Danthonia decumbens
Daucus carrota
Deschampsia cespitosa
Deschampsia flexuosa
Dianthus deltoides
Elymus repens
Epilobium angustifolium
Epilobium montanum
Epilobium palustre
Erophila verna
Euphrasia nemorosa
Euphrasia stricta
Festuca ovina
Festuca pratensis
Festuca rubra
Filipendula ulmaria
Filipendula vulgaris
Fragaria vesca
Fragaria viridis
Galium boreale
Galium saxatile
Galium uliginosum
Galium verum
Gentianella campestris
Geranium sylvaticum
Geum rivale
Geum urbanum
Glechoma hederacea
Gnaphalium sylvaticum
Helianthemun nummularium
Hieracium pilosella
Heiracium Sylvaticiformia
Hieracium Vulgatiformia
Hypericum maculatum
Hypericum perforatum
Hypochoeris maculate
Juncus articulatus
Juncus compressus
Juncus conglomeratus
Juncus effuses

Juncus ranarius
Juniperus communis
Knautia arvensis
Laserpitium latifolium
Lathyrus linifolius
Lathyrus palustris
Lathyrus pratensis
Leontodon autumnalis
Leucanthemum vulgare
Linum catharticum
Lotus corniculatus
Luzula campestris
Lychnis viscaria
Myosotis arvensis
Myosotis laxa
Myosotis ramosissima
Oxalis acetosella
Phleum pratense
Pimpinella major
Pimpinella saxifraga
Plantago lanceolata
Plantago major
Plantago media
Poa annua
Poa nemoralis
Poa pratensis
Polygala amarella
Polygala vulgaris
Potentilla anserina
Potentilla argentea
Potentilla erecta
Potentilla reptans
Potentilla tabernaemontani
Primula veris
Prunella vulgaris
Pyrola rotundifolia
Quercus robur
Ranunculus acris
Rhinanthus minor
Rosa canina
Rosa dumalis
Rosa villosa
Rubus idaeus
Rubus saxatilis
Rumex acetosa
Rumex acetosella
Rumex aquaticus
Rumex crispus
Sagina procumbens
Saxifraga granulata
Sedum acre
Sedum album
Sedum telephium
Silene nutans
Solidago virgaurea
Stellaria graminea
Stellaria media
Succisa pratensis
Tanacetum vulgare
Taraxacum erythrosperma
Taraxacum vulgare
Thymus serpyllum
Tragopogon pratensis
Trifolium arvense
Trifolium hybridum
Trifolium medium
Trifolium pratense
Trifolium repens
Urtica dioica
Vaccinium myrtillus
Vaccinium vitis-idaea
Veronica arvensis
Veronica chamaedrys
Veronica officinalis
Veronica scutellata
Veronica serpyllifolia
Vicia cassubica
Vicia cracca
Vicia lathyroides
Vicia sepium
Viola canina
Viola tricolor

Table S4. Mean observed species richness and standard deviation (SD) per habitat type for each taxon.

Group	Habitat type	Mean	SD
Bumblebees	Field border	3.38	1.63
	Big road	4.03	2.50
	Pasture	4.84	2.57
	Power line	4.62	1.54
	Small road	4.35	2.54
Butterflies	Field border	7.05	2.64
	Big road	6.34	3.48
	Pasture	10.16	4.16
	Power line	12.69	3.94
	Small road	8.47	4.45
Plants	Field border	10.30	3.39
	Big road	15.97	4.64
	Pasture	17.94	4.83
	Power line	19.06	5.94
	Small road	18.84	6.48

Table S5. **Results of the best model given in Table S6.** The reference habitat is road verges along big roads (big road). SNG= area of semi-natural pastures in the landscape, PL = Presence/absence of power-line corridors in the landscape (given values are for the reference: Presence), RD = road verge density in the landscape (given values are for the reference = high road verge density).

Response variable	**Explanatory**	**Estimate**	**Std.**	**z-value**	**Pr(>|z|)**
Bumblebee species richness	Intercept	1.41	0.06		
Butterfly species richness	Intercept	1.86	0.12		
	Field border	0.10	0.11	0.89	0.38
	Pasture	0.47	0.09	5.27	**<0.001**
	Power line	0.70	0.10	6.78	**<0.001**
	Small road	0.29	0.09	3.12	**<0.01**
	SNG	0.50	0.47	1.08	0.28
	PL	-0.02	0.09	-0.28	0.78
	RD	-0.16	0.08	-1.88	0.06
Plant species richness	Intercept	2.71	0.09		
	Field border	-0.44	0.08	-5.24	**<0.001**
	Pasture	0.12	0.06	1.91	0.06
	Power line	0.09	0.08	1.16	0.25
	Small road	0.17	0.06	2.76	**<0.01**
	SNG	-0.36	0.40	-0.91	0.36
	PL	0.18	0.07	2.47	**0.01**
	RD	<0.001	0.07	0.01	1.00

Table S6. AICc values for models explaining alpha diversity including explanatory variables and interactions. All models were generalized linear mixed models with the landscape as a random effect and were modelled with a Poisson distribution and a logit link. The lowest AICc value was used to select the model. When ΔAICc <2 the simplest model was selected. The best model is the first one presented for each analysis. Candidate models are organized from smallest to largest AICc. H= habitat type, SNG= area of semi-natural pastures in the landscape, PL= Presence/absence of power-line corridors in the landscape, RD= road verge density in the landscape (high/low). The colons indicate an interaction between the explanatory variables. If the model is not shown, it is due to non-convergence.

Response variable	**Candidate model**	**AICc**	**ΔAICc**
Bumblebee species richness	Null model	595.39	0
	H + SNG + PL + RD	599.88	4.49
	H + SNG + PL + RD + SNG:RD	601.34	5.95
	H + SNG + PL + RD + PL:RD	601.96	6.57
	H + SNG + PL + RD + SNG:PL	602.16	6.77
	H + SNG + PL + RD + H:RD	604.06	8.67
	H + SNG + PL + RD + H:PL	605.87	10.48
Butterfly species richness	H + SNG + PL + RD	741.54	0
	H + SNG + PL + RD + PL:RD	741.83	0.29
	H + SNG + PL + RD + SNG:RD	742.97	1.43
	H + SNG + PL + RD + SNG:PL	743.77	2.23
	H + SNG + PL + RD + H:SNG	744.20	2.66
	H + SNG + PL + RD + H:PL	745.55	4.01
	H + SNG + PL + RD + H:RD	750.10	8.56
	Null model	792.28	50.74
Plant species richness	H + SNG + PL + RD	794.70	0
	H + SNG + PL + RD + SNG:RD	795.53	0.83
	H + SNG + PL + RD + SNG:PL	796.09	1.39
	H + SNG + PL + RD + PL:RD	796.82	2.12
	Null model	853.37	58.67

Table S7. Results from the pairwise PERMANOVA analysis exploring differences in the community composition between pairs of habitat types for all species groups. P-values were adjusted with the Holm method. P-values in bold are significant at the 0.05 level.

Group	Habitat 1	Habitat 2	p-val	Adjusted p-val
Bumblebees	Field border	Big road	**<0.001**	**<0.01**
	Field border	Pasture	**<0.01**	**0.05**
	Field border	Power line	0.01	0.05
	Field border	Small road	**<0.001**	**<0.01**
	Big road	Pasture	0.24	0.47
	Big road	Power line	0.07	0.27
	Big road	Small road	**<0.01**	**0.05**
	Pasture	Power line	0.09	0.27
	Pasture	Small road	**<0.001**	**<0.01**
	Power line	Small road	0.39	0.47
Butterflies	Field border	Big road	**<0.01**	**<0.01**
	Field border	Pasture	**<0.001**	**<0.01**
	Field border	Power line	**<0.001**	**<0.01**
	Field border	Small road	**<0.01**	**<0.01**
	Big road	Pasture	**<0.001**	**<0.01**
	Big road	Power line	**<0.001**	**<0.01**
	Big road	Small road	**<0.001**	**<0.01**
	Pasture	Power line	**<0.001**	**<0.01**
	Pasture	Small road	**<0.001**	**<0.01**
	Power line	Small road	**<0.01**	**<0.01**
Plants	Field border	Big road	**<0.001**	**<0.01**
	Field border	Pasture	**<0.001**	**<0.01**
	Field border	Power line	**<0.01**	**<0.01**
	Field border	Small road	**<0.001**	**<0.01**
	Big road	Pasture	**<0.001**	**<0.01**
	Big road	Power line	**<0.001**	**<0.01**
	Big road	Small road	**<0.001**	**<0.01**
	Pasture	Power line	**<0.001**	**<0.01**
	Pasture	Small road	**<0.001**	**<0.01**
	Power line	Small road	**<0.001**	**<0.01**

Table S8. AICc values for PERMANOVA analyses exploring differences in community composition among habitat types and how the amount of habitat in the landscape affects them. All models included the identity of the landscape as a random component. The lowest AICc value was used to select the model. When ΔAICc <2 the simplest model was selected. The best model is the first one presented for each analysis. Candidate models are organized from smallest to largest AICc. H= habitat type, SNG= area of semi-natural pastures in the landscape, PL= Presence/absence of power line corridors in the landscape, RD= road verge density in the landscape (high/low).

Response variable	**Candidate model**	**AICc**	**ΔAICc**
Bumblebee communities	Null model	-145.93	0.00
	H + SNG + PL + RD	-144.82	1.12
	H + SNG + PL + RD + SNG:RD	-144.51	1.42
	H + SNG + PL + RD + SNG:PL	-144.00	1.93
	H + SNG + PL + RD + PL:RD	-142.84	3.09
	H + SNG + PL + RD + H:RD	-139.84	6.09
	H + SNG + PL + RD + H:PL	-139.84	6.09
	H + SNG + PL + RD + H:SNG	-138.84	7.09
Butterfly communities	H + SNG + PL + RD + SNG:RD	-191.11	0.00
	H + SNG + PL + RD	-190.99	0.12
	H + SNG + PL + RD + SNG:PL	-190.74	0.37
	H + SNG + PL + RD + PL:RD	-189.30	1.81
	Null model	-187.75	3.36
	H + SNG + PL + RD + H:RD	-187.12	4.00
	H + SNG + PL + RD + H:PL	-187.12	4.00
	H + SNG + PL + RD + H:SNG	-184.64	6.48
Plant communities	H + SNG + PL + RD	-175.89	0.00
	H + SNG + PL + RD + SNG:RD	-175.72	0.17
	H + SNG + PL + RD + SNG:PL	-174.96	0.94
	H + SNG + PL + RD + PL:RD	-174.43	1.46
	H + SNG + PL + RD + H:RD	-171.22	4.67
	H + SNG + PL + RD + H:PL	-171.22	4.67
	H + SNG + PL + RD + H:SNG	-170.11	5.79
	Null model	-160.66	15.23

Table S9. Results of the indicator species analysis that aimed to assess whether there were species with strong associations to specific habitat types.

Group	Habitat	Species	stat	p
Bumblebee	Big road	*Bombus subterraneus*	0.2	0.04*
	Pasture	*Bombus ruderarius*	0.3	0.01*
	Power line + Small road	*Bombus pratorum*	0.2	0.01*
	Big road + Pasture + Power line + Small	*Bombus pascuorum*	0.3	0.01**
Butterflies	Power line	*Plebejus argus*	0.5	<0.001*
		Boloria selene	0.5	<0.001*
		Plebejus idas	0.4	<0.001*
		Brenthis ino	0.3	<0.001*
		Gonepteryx rhamni	0.3	<0.001*
		Plebejus optilete	0.3	<0.01**
		Argynnis paphia	0.3	<0.01**
		Argynnis adippe	0.3	<0.01**
		Boloria euphrosyne	0.3	<0.001*
	Field border + Power line	*Inachis io*	0.3	0.01*
	Field border + Small road	*Pieris napi*	0.3	<0.01**
	Pasture + Power line	*Coenonympha arcania*	0.4	<0.001*
		Lycaena phlaeas	0.3	<0.01**
		Coenonym. pamphilus	0.2	0.04*
	Pasture + Power line + Small road	*Melitaea athalia*	0.2	0.01*
Plants	Field border	*Cirsium arvense*	0.6	<0.001*
		Elymus repens	0.5	<0.001*
		Alopecurus pratensis	0.4	<0.001*
		Filipendula ulmaria	0.3	<0.01**
		Myosotis arvensis	0.3	<0.01**
		Urtica dioica	0.3	<0.01**
		Festuca pratensis	0.2	0.04*
	Big road	*Rumex acetosella*	0.4	<0.001*
		Arrhenatherum	0.4	<0.001*
	Pasture	*Veronica chamaedrys*	0.4	<0.001*
		Galium verum	0.4	<0.001*
		Filipendula vulgaris	0.4	<0.001*
		Alchemilla	0.4	<0.01**
		Pimpinella saxifraga	0.3	<0.01**
		Rumex acetosa	0.3	<0.01**
		Plantago lanceolata	0.2	0.02*
	Power line	*Vaccinium vitis-idaea*	0.5	<0.001*
		Calluna vulgaris	0.5	<0.001*

	Rubus idaeus	0.5	<0.001*
	Vaccinium myrtillus	0.4	<0.001*
	Betula pendula	0.4	<0.001*
	Juncus effusus	0.4	<0.001*
	Deschampsia flexuosa	0.4	<0.001*
	Convallaria majalis	0.3	<0.01**
	Achillea ptarmica	0.3	<0.01**
	Carex panacea	0.3	0.02*
	Succissa pratensis	0.3	0.01*
	Deschampsia	0.3	<0.01**
	Hypericum maculatum	0.3	<0.01**
	Carex nigra	0.3	0.01*
	Campanula	0.2	0.02*
	Danthonia decumbens	0.2	0.03*
	Cirsium palustre	0.2	0.02*
	Carex pallescens	0.2	0.04*
Small roads	*Plantago major*	0.5	<0.001*
	Poa annua	0.4	<0.001*
Big road + Power line	*Galium boreale*	0.2	0.02*
Pasture + Power line	*Rhinanthus minor*	0.2	0.02*
	Luzula campestris	0.2	0.03*
Pasture + Small road	*Trifolium repens*	0.4	<0.001*
	Prunella vulgaris	0.3	<0.01**
Power line + Small road	*Fragaria vesca*	0.2	0.02*
Big road + Pasture + Small road	*Achillea millefolium*	0.5	<0.001*
	Leontodon autumnalis	0.3	<0.01**
	Lotus corniculatus	0.2	0.03*
	Trifolium pratense	0.2	0.04*
Big road + Power line + Small road	*Potentilla erecta*	0.3	<0.001*
Pasture + Power line + Small road	*Anthoxanthum*	0.3	<0.01**
	Viola canina	0.2	0.01*
Field border + Big road + Pasture + Small	*Taraxacum vulgare*	0.3	<0.01**
Big road + Pasture + Power line + Small	*Agrostis capillaris*	0.4	<0.001*
	Trifolium medium	0.3	<0.01**

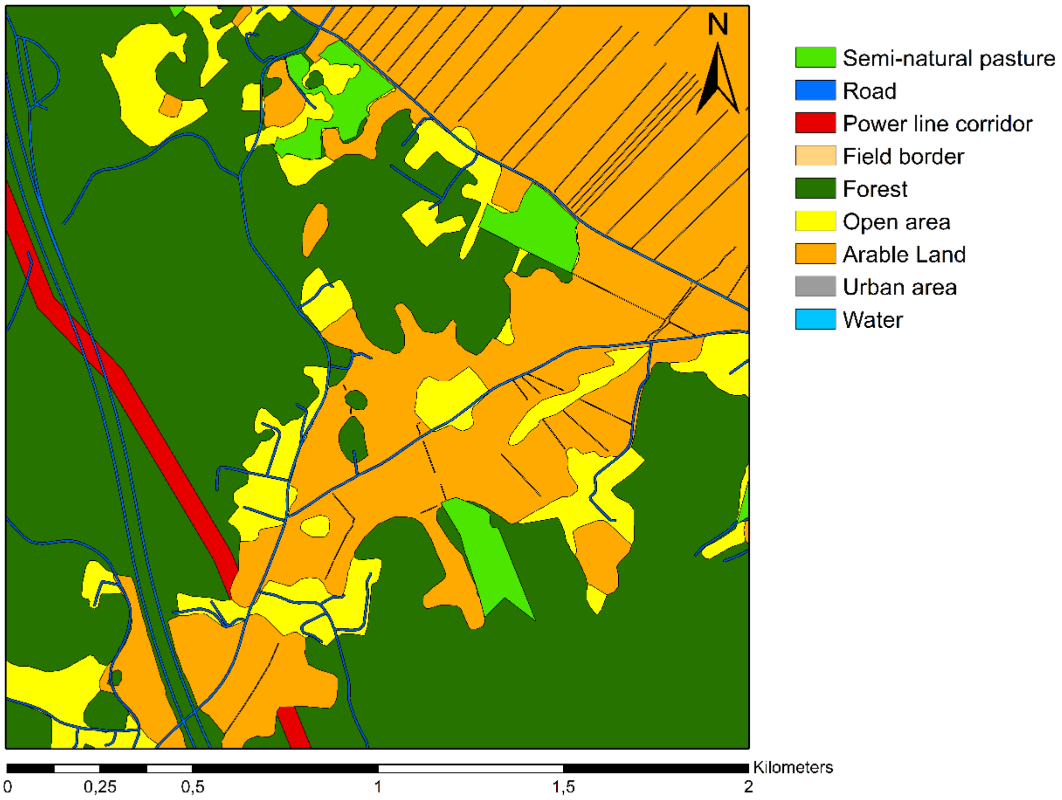

Figure S1. Example landscape illustrating how landscape composition (area of different land-cover types) was measured. All landscapes had similar area of forest and agricultural land, while the area of semi-natural pastures and linear infrastructure habitats differed as seen in Figure 1b.

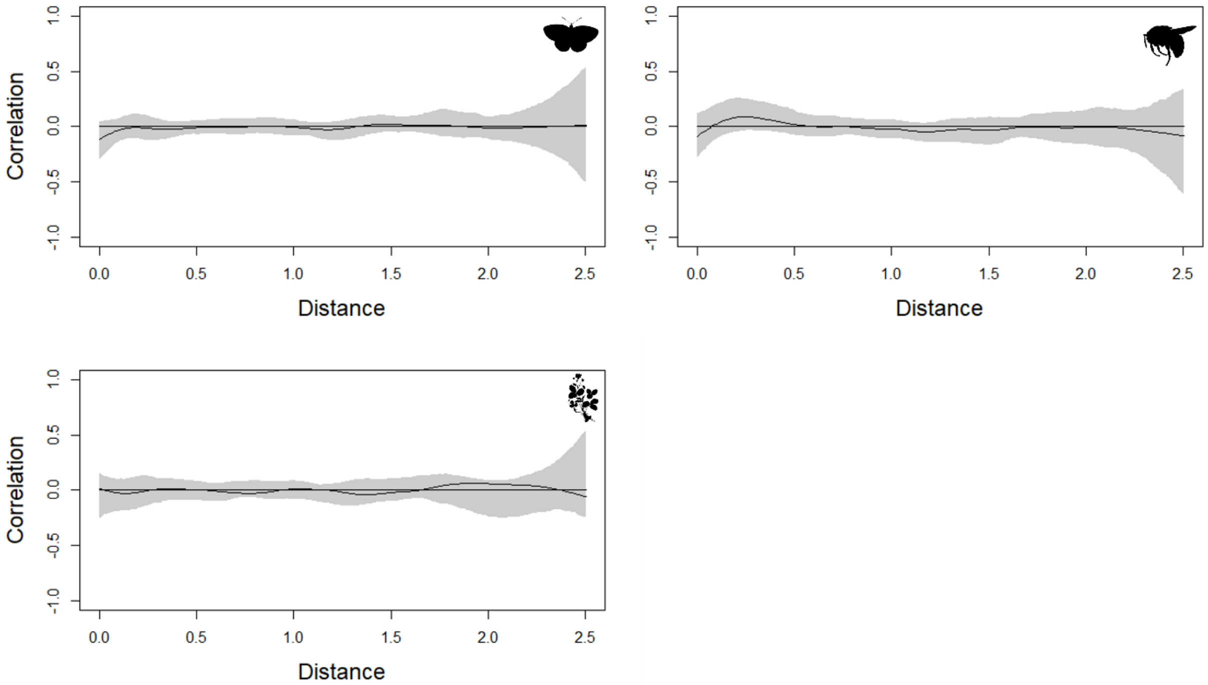

Figure S2. Spline correlograms showing the absence of spatial autocorrelation in the residuals of the alpha-diversity models for (a) butterflies, (b) bumblebees, and (c) vascular plants. The figures were created with the function 'spline.correlog' in the package *ncf*. The confidence intervals represent the quartiles.

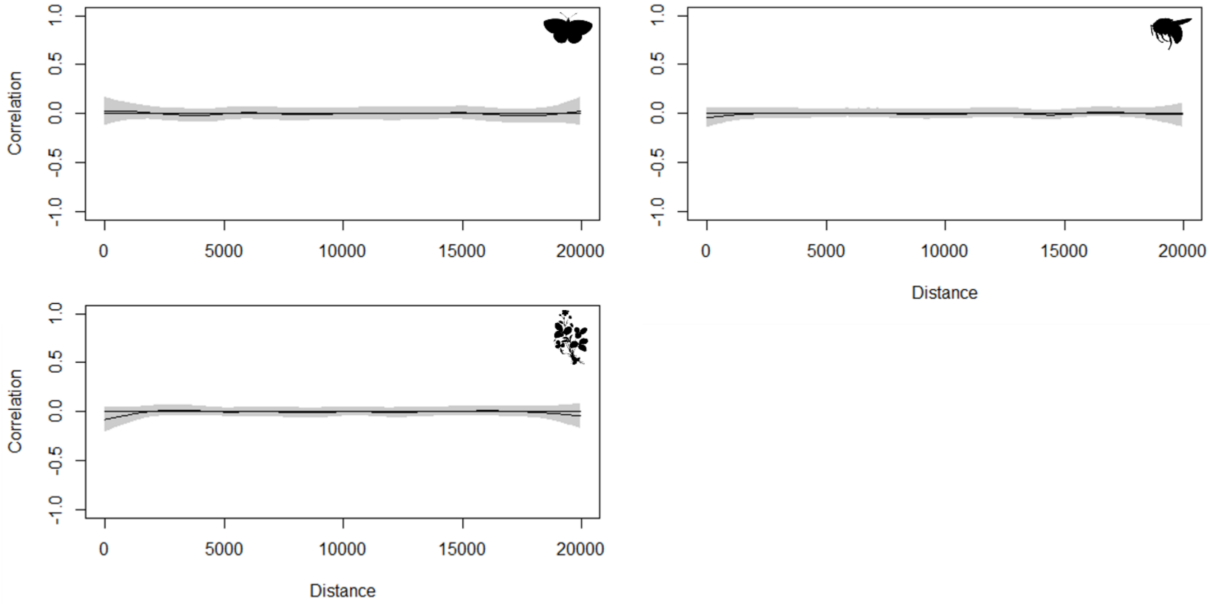

Figure S3. Spline correlograms based on the Bray-Curtis distance between species' assemblages and the centroid of transects. The figures show the absence of spatial autocorrelation for (a) butterflies, (b) bumblebees, and (c) vascular plants. The figures were created with the function 'spline.correlog in the package *ncf*. The confidence intervals represent the quartiles.

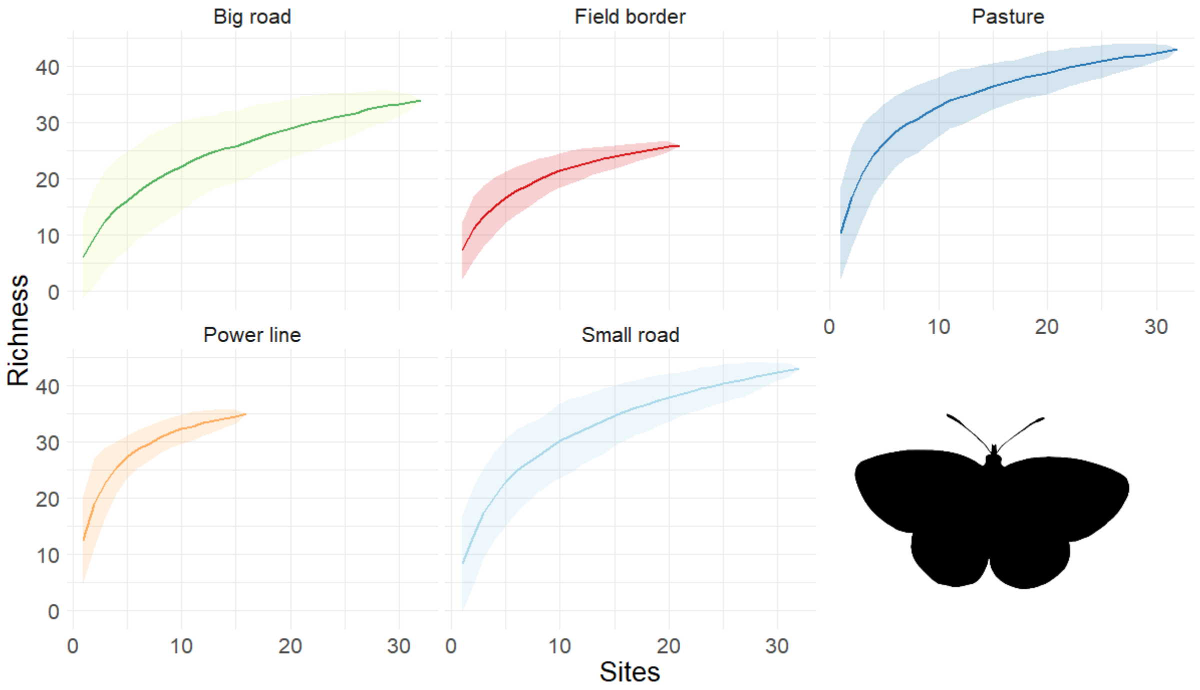

Figure S4. Species accumulation curves in the five grassland habitat types for butterflies. The figures were created with the function 'specaccum' in the package *vegan and* using the method 'random'. The confidence intervals represent the standard deviation (standard error of the estimate).

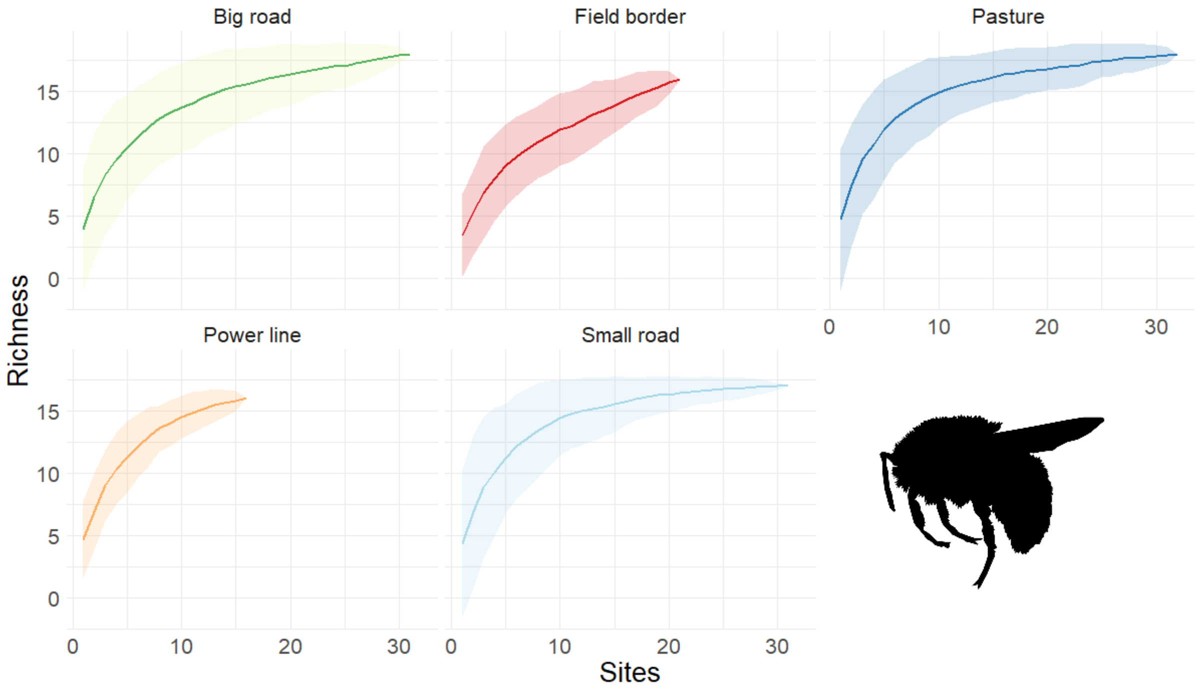

Figure S5. Species accumulation curves in the five grassland habitat types for bumblebees. The figures were created with the function 'specaccum' in the package *vegan and* using the method 'random'. The confidence intervals represent the standard deviation (standard error of the estimate).

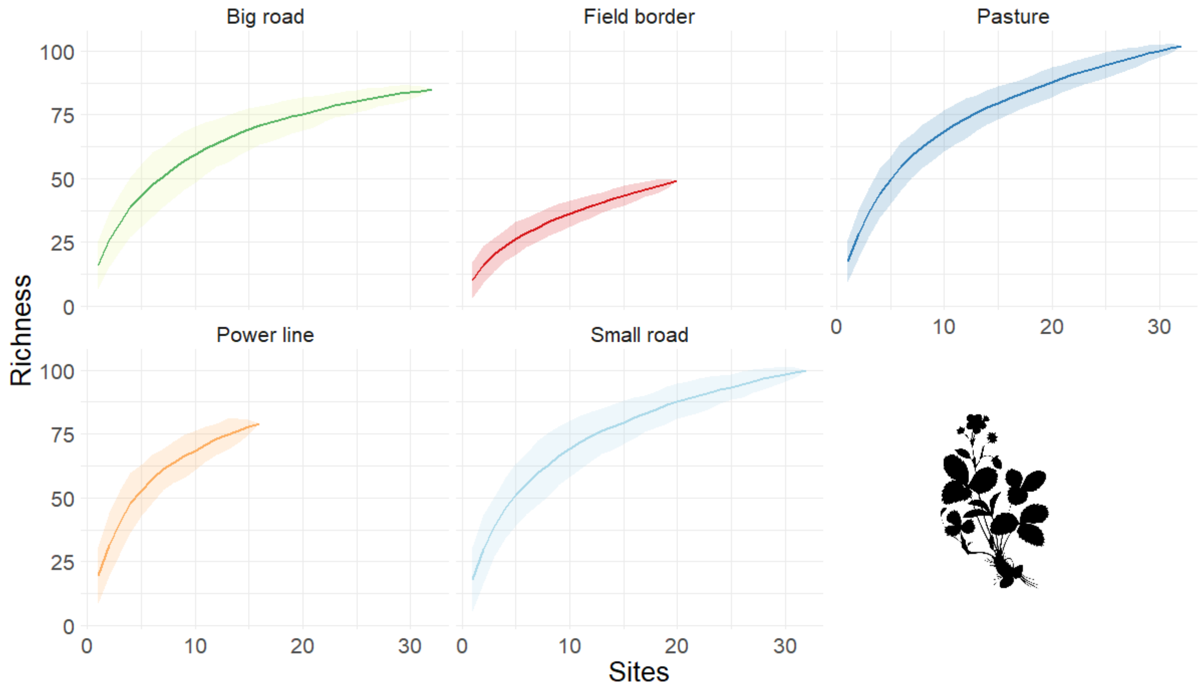

Figure S6. Species accumulation curves in the five grassland habitat types for vascular plants. The figures were created with the function ‘specaccum’ in the package *vegan and* using the method ‘random’. The confidence intervals represent the standard deviation (standard error of the estimate).

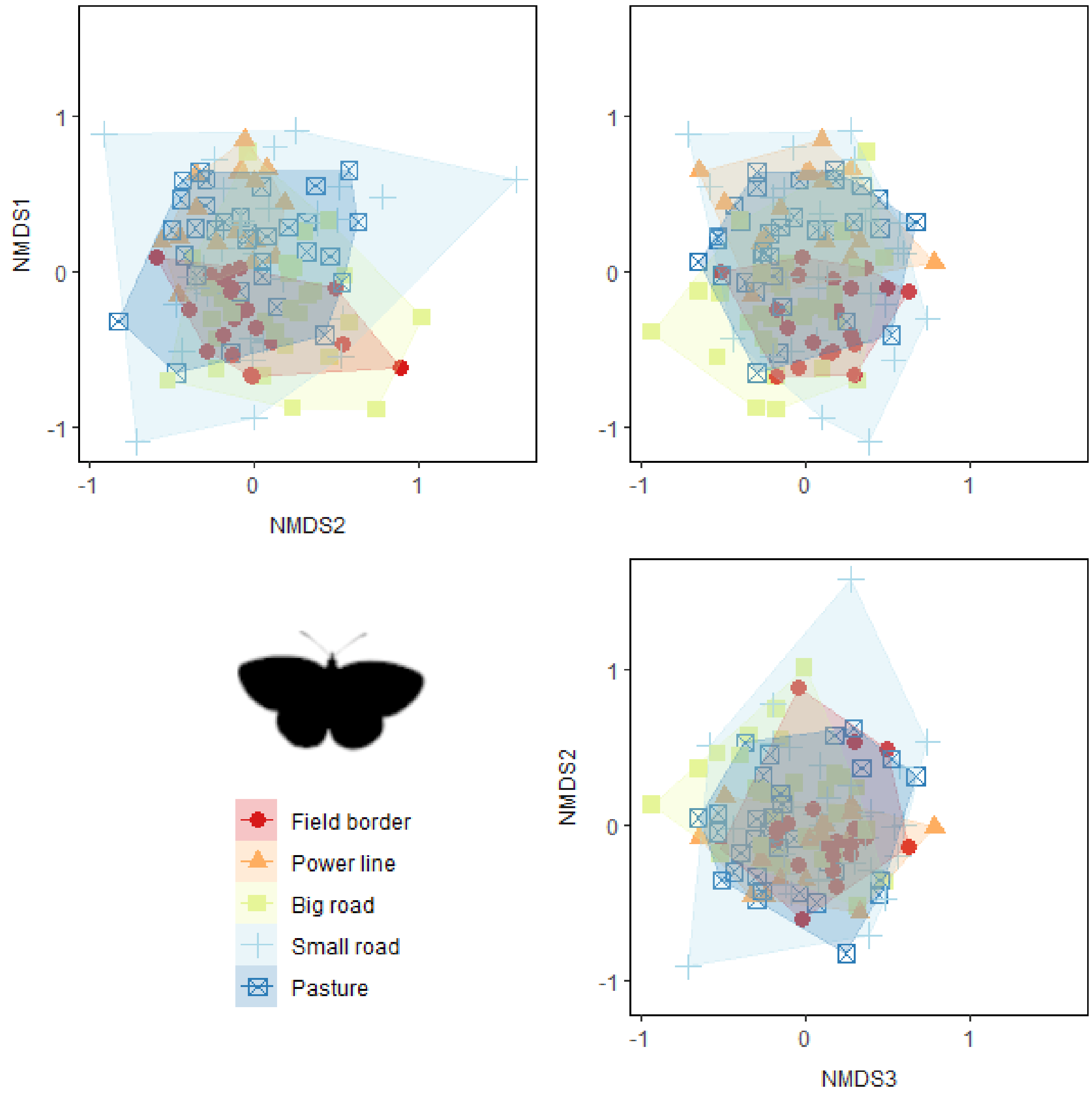

Figure S7. Non-metric multidimensional scaling (NMDS) analysis for butterflies (stress= 0.20) in the five types of grassland habitats. The figure shows differences and similarities in community composition among habitat types for butterflies in three dimensions (NMDS1, NMDS2, and NMDS3).

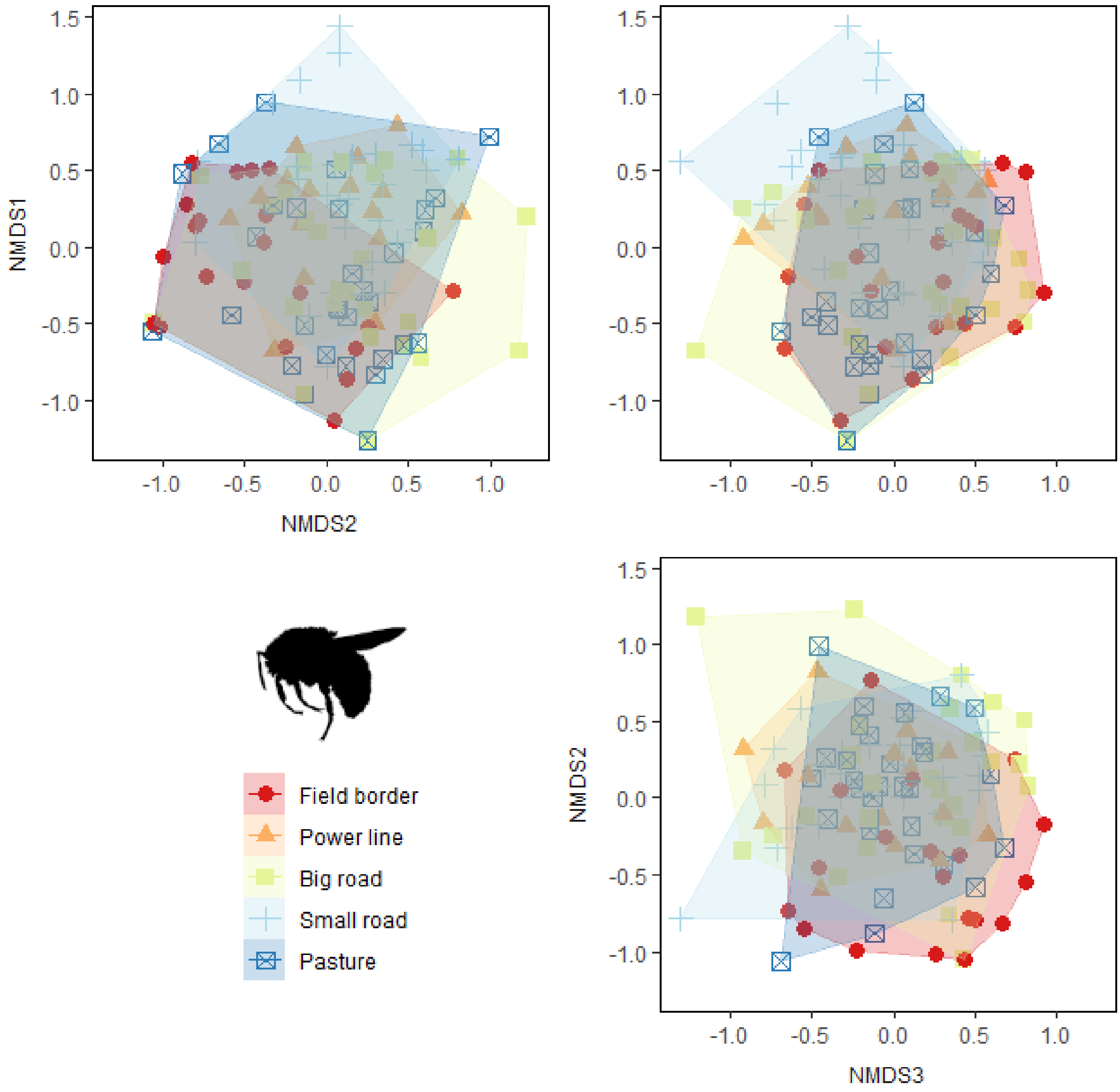

Figure S8. Non-metric multidimensional scaling (NMDS) analysis for bumblebees (stress= 0.17) in the five types of grassland habitats. The figure shows differences and similarities in community composition among habitat types for bumblebees in three dimensions (NMDS1, NMDS2, and NMDS3).

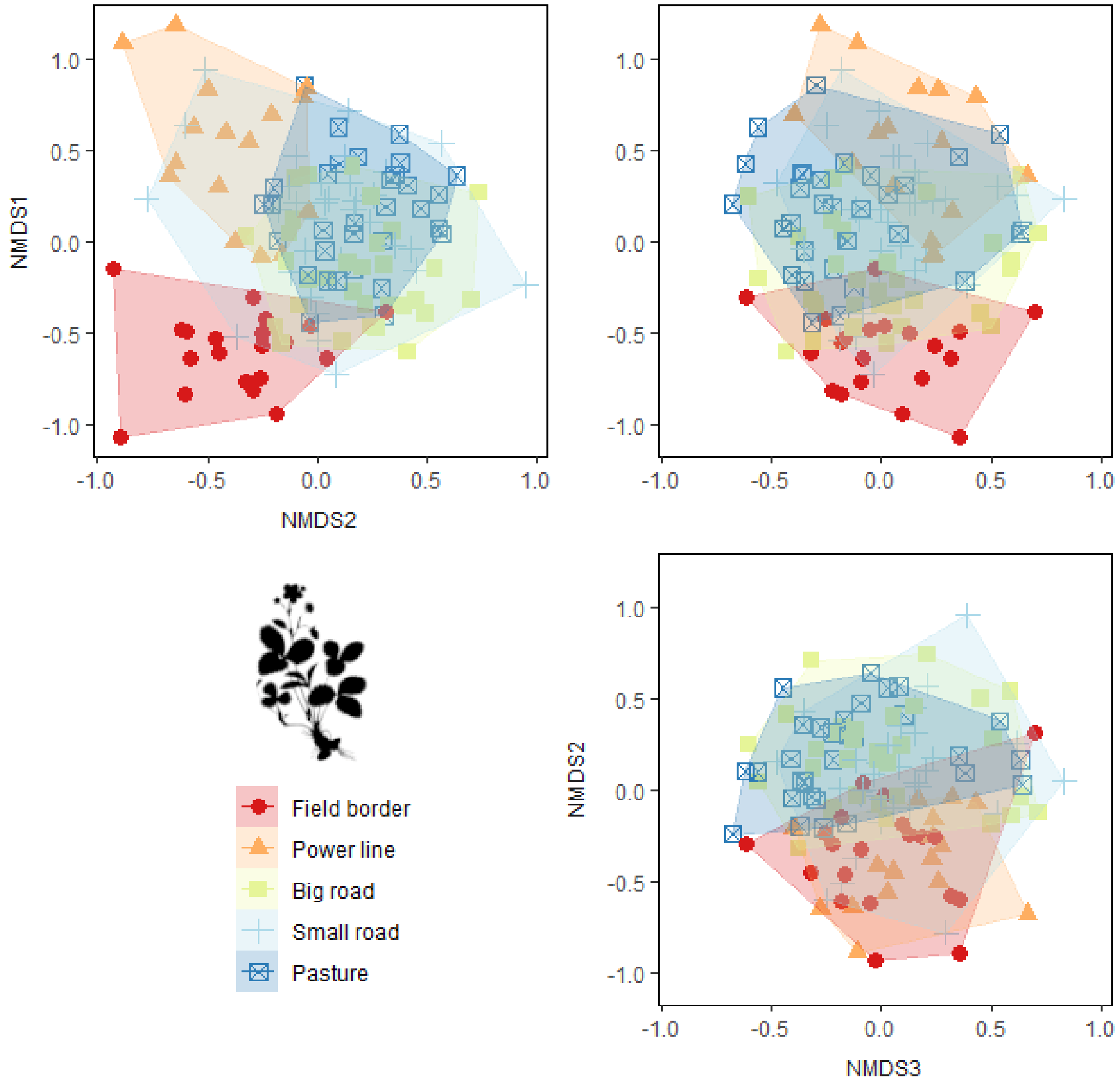

Figure S9. Non-metric multidimensional scaling (NMDS) analysis for plants (stress= 0.19) in the five types of grassland habitats. The figure shows differences and similarities in community composition among habitat types for plants in three dimensions (NMDS1, NMDS2, and NMDS3).

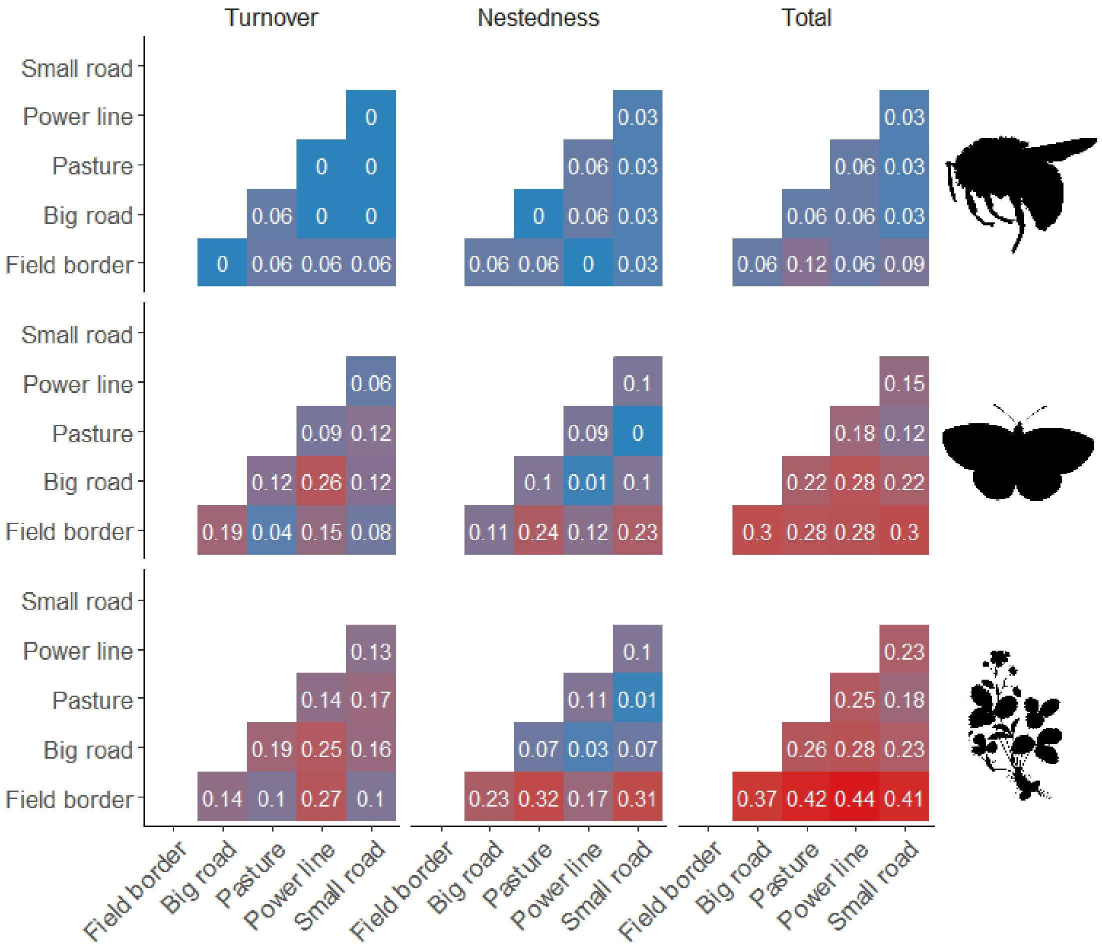

Figure S10. Pairwise beta diversity (βsor) partitioned into the spatial species turnover (βsim) and nestedness (βnes) components for all species groups (from top to bottom: bumblebees, butterflies, and plants).